THE
JOURNAL OF ECOLOGY

VOLUME XX

THE

JOURNAL OF ECOLOGY

EDITED FOR THE

BRITISH ECOLOGICAL SOCIETY

BY

A. G. TANSLEY

VOLUME XX

1932

WITH TWENTY-NINE PLATES, AND NUMEROUS
FIGURES IN THE TEXT

CONTENTS

vi   *Contents*

CADER IDRIS: A STUDY OF CERTAIN PLANT COMMUNITIES IN SOUTH-WEST MERIONETHSHIRE

By E. PRICE EVANS.

(With Plates I–IV and five Maps in the Text.)

CONTENTS.

1. INTRODUCTION.

THE area dominated by Cader Idris ranks as one of the most interesting geological and botanical regions in the British Isles: for the diversity of its geological and topographical features, for the variety of its flora, especially of its cryptogamic flora, and (in certain parts) for the luxuriance of its vegetation, it is hardly surpassed. In consequence it has attracted the attentions of the field geologist and the field botanist in the past, and certain aspects of its natural history, but more especially of its geology, have been carefully studied.

The object of this paper is to give the results of a more or less detailed study of the vegetation of a belt transect across (up) the north-facing slope of the Cader Range from the valley bottom to the summit plateau and the inferences that may be drawn therefrom.

2. THE CADER IDRIS LOCAL AREA.

In order to clear the ground it will be necessary to consider the leading geological and geographical features of the area as a whole, with special reference to those aspects that have a direct bearing on the vegetation.

Geologically, the Cader area compares closely with Snowdonia (Map 1), and may be regarded as a part of it; but topographically, it is a distinct entity. It is a quadrangular block of mountainous country situated at the south-west corner of the county of Merioneth. The mountain block is bounded on the west by Cardigan Bay and on the east by the line of the old "radial" valleys (Dulas and Mawddach-Eden); it is separated from the central uplands to the south by the valley of the Dovey, and is cut off from the other parts of Snowdonia to the north by the Mawddach-Wnion. A third valley (also with a north-east to south-west trend)—the Talyllyn Valley—cuts the mountain block into two nearly equal parts (Map 2).

Proximity to the sea and all that it implies with respect to winds, temperature and rainfall, a very varied topography including deep sheltered valleys, open moorlands and exposed craggy heights, and the presence of rocks of diverse chemical and physical nature, seem to be the most important physiographical factors determining the luxuriance, variety and distribution of the vegetation.

(a) Rainfall.

The following data for places within (or very near to) the Cader Idris area are taken from British rainfall statistics for the year 1925.

No figures are available for the elevated parts; but the three cwms (in which lie Llyn Cau, Llyn y Gader and Llyn Aran respectively) which are on the immediate lee side of the highest points are probably the localities where the rainfall is greatest. At about 1500 ft. (457 m.) in similar situations in the

MAP 1. North-western Wales, showing the relation of Cader Idris to Snowdonia, the middle post-glacial (Atlantic) coast-line, and the distribution of radial and transverse valleys.

Snowdon district (**1**) the rainfall is roughly 150 in. (381 cm.); the rainfall upon Plynlimmon averages from 70 in. (178 cm.) to 80 in. (203 cm.) (**2**); and it is therefore probable that the rainfall of the highest parts of Cader Idris exceeds 100 in. (254 cm.).

	Altitude of gauge ft.	Rainfall for 1925 in. mm.	Average rainfall (over 20 years)	Rain days (with 0·01 in. or more)	Wet days (with 0·04 in. or more)
Towyn: Ynys-y-Maengwyn	14	42·50 (1080)	—	194	162
Bronffynnon	180	41·05 (1043)	44·2	202	166
Peniarth	25	49·58 (1259)	—	212	185
Talyllyn Rectory	270	67·89 (1724)	—	188	168
Dolgelley: Dol'rhyd	100	59·82 (1519)	—	229	180
Bryntirion	50	61·08 (1551)	58·8	224	192
Trawsfynydd Camp	800	68·20 (1732)	67·0	210	195
Aberdovey: Plas Penhelig	120	46·29 (1176)	—	—	—
Pennal: Talgarth	125	59·11 (1501)	—	—	158
Dinas Mawddwy	250	69·45 (1764)	65·2	—	—

(b) The "solid" geology.

Stratigraphically, the area is composed of an almost complete succession of Ordovician strata ranging from the Arenig Beds, which rest on those of the Upper Cambrian to the immediate south of the Mawddach estuary, through Llandeilo Beds to the Bala formations which pass under the Silurian strata on the southern edge of the area (Map 2). In addition to sedimentary rocks, igneous rocks are present in different parts of the succession: volcanic rocks occur at four distinct stratigraphical horizons, and intrusive rocks may appear at almost any stratigraphical level. The sedimentary rocks are mostly grits or slates, intercalated with ash bands or containing in parts a large amount of ashy material; the volcanic rocks are mostly tuffs, lavas or ashes; and the intrusive rocks are mostly dolerites or granophyres. The igneous rocks range from acid through intermediate to basic (**3, 4** a).

Owing to the prevailing high dip and to the pronounced erosion that has taken place markedly along the shatter belts, with the consequent exposure of rocks of varying chemical composition, the distribution of the rocks has a direct bearing on the nature of the vegetation. The slaty, the intrusive, and the acid volcanic rocks, may be described as poor in respect to floristic variety; but the basic volcanic rocks, in particular the "pillow lavas," are markedly rich in plants. The presence of distinct calcicole species on the basic "pillow lavas" is one of the most striking features of the vegetation of this interesting area.

(c) Topography and geography.

The relation between topography and geological structure is strikingly illustrated in the surface features of the Cader area. The whole mass stands out in comparatively high relief by virtue of the presence of hard resistant igneous masses: it is separated from the adjacent areas by deep valleys that

Phot. 1. Cader Idris, from the north-west. The main escarpment is due to the granophyre sill forming Mynydd Moel (M), Foxes' Path (F) and Cyfrwy (Saddle: C). On Pen y Gader (summit: P) higher strata appear. Llyn y Gader occupies the hollow under (F, P, C): Llyn Aran is under (east of) M: the summit-plateau occupies the dip slope between M and P. 5–5 marks the outcrop of the Lower Basic Group (including the band of "pillow lava"): it continues to the left through the Upland Valley between M and the left-hand 4. 4–4 Cefn-hir ashes with dolerites; 3–3 Bifidus slates; D dolerite; and G granophyre. The lower part of the transect is to the left (east) of the area shown in the foreground of the photo. The western end of Mynydd y Gader is marked D 3–4 (extreme left).

EVANS—CADER IDRIS: A STUDY OF CERTAIN PLANT COMMUNITIES IN SOUTH-WEST MERIONETHSHIRE

follow important lines of structure; and it owes its striking scenery to the diversity of surface features resulting from the differential action of the weathering agents on the usually hard igneous masses and on the relatively softer slaty rocks that together make up its structure.

Ancient platforms. "From a high view-point there is no topographic feature in the district more striking than the deeply dissected 2000 ft. plateau, that extends southwards from the Cader Idris-Aran range into mid-Wales, declining gently in that direction. The age of this 2000 ft. peneplain and its mode of formation are unknown" (4 *b*); but it is certainly a very ancient feature and it was in existence long before the Glacial Period. Cader Idris, the Aran Peaks, and Plynlimmon rise high above this plateau. There are other platforms at lower levels, notably those between 1100 ft. and 1600 ft. (335 m. and 488 m.) and those at about 500 ft. (152 m.): some of these almost certainly bear a relation to ancient systems of drainage. These lower platforms often have a thin covering of "drift" and are thus also pre-Glacial in origin. The gentle slope and, in some cases, the "drift," render the drainage defective—a state of affairs that results in the accumulation of peat and in the growth of plants characteristic of acid humus.

Drainage. The present system of drainage is comparatively simple, governed as it is by the main lines of structure. The block as a whole drains westwards by means of rather sluggish main streams flowing with the grain (north-east to south-west) of the land, fed by generally swift tributary streams flowing across the grain. Some of the tributary streams may indicate the direction of a former system of drainage—a "radial" system that may have prevailed before the present system draining to the west along the main fault lines was developed. "The original drainage system of North Wales was a radial system, the centre of which lay in the high ground around the sources of the Conway. Subsequently a series of transverse valleys was formed which divided the radial system into sections, and each of the principal transverse valleys now carries away the drainage of one of these sections" (5) (Map 1).

Glaciation. The Cader area is a region of high rainfall at the present day and doubtless it was a region of heavy precipitation during a part, at least, of the Glacial Epoch: the corries (or cwms), the corrie lakes held up by the moraines (Pl. II, Phot. 2), the "hanging" valleys, the U-shaped valley bottoms, and other evidence of local glaciation are prominent features of the landscape[1]. The corries and the glaciated valleys of Talyllyn and of the Mawddach are magnificent examples of their kind, rivalling in grandeur similar features in other parts of North Wales. "It is only of late that the great importance of the cwm topography has been realised in England. This is surprising in view of the magnificent clusters of cwms ('karling') which constitute Snowdonia and

---

[1] At the same time the gouging influence of the ice must not be over-estimated: before the Glacial Epoch the present rivers had cut steep-sided narrow valleys in the uplifted plateau. Erosion during the Glacial Period emphasised and slightly modified the form of these valleys (6).

Cader Idris. The latter especially is a perfect example of a small karling. In fact, one might safely say that the most striking feature in glacial topography in Great Britain has attracted least attention. On a recent visit to Barmouth the resemblance in the topography to that of Granite harbour (East Antarctica) was almost ludicrous. The same broad valley—the same riegel and high level terraces or alp plateaux; the rounded nunakoller and cuspate nunatakker; and on the slopes of the bounding walls the same magnificent cwms[1]."

There are also definite indications that the district was invaded by ice from the outside: the *roches moutonnées*, the striated rocks, the erratics, and in one case a glaciated pavement (4 *b*) at the summit of an isolated hill about 1328 ft. (405 m.) high show that the region was overridden by ice to a considerable height. "Although monoglacialists would refer these effects to three successive phases of *one* period, there is an increasing weight of evidence in favour of at least two such periods separated by one of genial climatic conditions. That being so, it is tempting, though not necessarily correct, to refer the regional effects in North Wales to a period of maximum glaciation and the local phenomena to a later, less rigorous cold period" (4 *b*).

At the time of maximum glaciation it is probable that the district was devoid of vegetation, though it is possible that some arctic species may have maintained a precarious foothold on some of the points that stood out as "nunataks." In this connection it is of the greatest interest to note that the present arctic-alpine flora of North Wales, whatever its origin may be, differs in important respects from that of the north of England: certain plants characteristic of that area are not present in Snowdonia or in the Cader area (see Discussion, p. 44).

Post-Glacial deposits. Three sets of deposits—the river terraces of the valley floors, the upland or moorland peats, and the submerged forests of the foreshore—indicate important geological or climatic changes that have taken place within the area since the close of the Glacial Period (*c.* 10,200 B.C.).

During the closing stages of the Glacial Epoch the rivers would have a large volume of water but would carry a light load owing to the frozen state of the ground: this would enable them to excavate their valleys and carry away the glacial débris. With the amelioration of the climate and the consequent increase of denudation the rivers would carry a heavy load and would deposit the material on the valley floor, forming alluvial flats, relics of which remain, and are known as river terraces (7 *a*). Such deposits are best developed in the upper valley of the Wnion just outside the eastern edge of the area; but they are small and have little bearing on the study of the vegetation except in so far as they may be indicative of a climatic change (perhaps the occurrence of a Pluvial or Rainy Epoch) in the immediate post-Glacial Period.

The upland or moorland peats are deposits ranging from a few inches to about 5 ft. (152 cm.) in thickness. Some of them show traces of a "forest" bed

---

[1] **Griffith Taylor** in the *Geog. Journ.* vol. **44**, No. 6, Dec. 1914.

Phot. 2. Cader Idris, from Llyn y Gader. G = granophyre, with Llyn y Gader mudstones (dark) above.
D = dolerite, with a thin slate band above. 7′ = basal ashes of the Upper Basic Group. f–f = fault gully.
In the foreground is the moraine that holds up the water of the corrie lake; to the left is the granophyre-
scree of Foxes' Path. Apart from the Chomophytes, the vegetation ranges from the open communities
of the moraine and the screes, through transitional communities—generally Gramino-Vaccinieta—to climax
grassland (Festucetum ovinae). *Cryptogramme crispa* is abundant on the talus slope facing the observer.

at or near the base, and in one case within this transect at an elevation between 1750 ft. and 1800 ft. (534–549 m.) the buried wood consists mainly of *Salix* and *Betula*. The basal layers of some of these peats are probably pre-Atlantic deposits. The peaty layers immediately overlying the "forest" layer may thus indicate the change from the dry Boreal to the moist Atlantic Period which occurred during epi-Palaeolithic time or just before the beginning of the "Neolithic" Period in Britain (see table, p. 46).

The submerged forests consist of alternating strata of estuarine silt and marsh soil with "forest" remains which occur under the coastal flats and strands and range from about 10 to 60 ft. (3–18 m.) below the present level of high water. These deposits were laid down during an episode in the geological history of the country known as the "Neolithic submergence."

"*Neolithic submergence.*" After the retreat of the ice-sheet from Cardigan Bay morainic material was left behind forming low-lying swampy land through which the rivers meandered to empty themselves into the sea some miles west of their present outlets (Map 1). This old land is the Cantref y Gwaelod[1] of the Legends, one of the best known of the lands which, according to these folk-tales, were inundated by the sea (Map 2). A forest bed occurs on parts of the foreshore at about 10–15 ft. (3–5 m.) below the present high-water mark and a bed of peat has been proved nearly 60 ft. (18 m.) below high water at the mouth of the Mawddach. Owing to the general absence of borings or excavations in the coastal flats of this area there is little direct evidence of the nature and the succession of these deposits known collectively as submerged forests. (For information on the nature of the wood in these forests see p. 45.)

Geological opinion, based largely on stratigraphical considerations, seems to favour a relatively rapid period of depression to cover the time represented by the submerged forests of Britain in general. "It is useless to pretend to any exact calculations as to the time needed for the formation of these alternating strata of estuarine silt and marsh soil; but looking at the whole of the evidence without bias either way, it seems that an allowance of 1000, or at most 1500, years would be ample time to allow. A period of 1500 years may therefore be taken to cover the whole of the changes which took place during the period of gradual submergence. If this is approximately correct, the date at which the submergence began was only 5000 years ago, or about 3000 B.C." (**8**). This view is confirmed, at least as far as the last phase of the movement of depression is concerned, by a study of the geology of the Dovey Flats: "it appears therefore that only relatively rapid subsidence is adequate to produce the conditions under which the vegetation of the Borth submerged forest grew" (**6**).

Archaeological evidence shows that (Late) "Neolithic" Man was in occupation before the final submergence; the absence of metal suggests that this event took place before the "Bronze Period"; but the final change must

[1] Engl. = The Lowland Hundred.

have occurred, on the coastal flats of this area, at a time sufficiently near for the ancestors of the present inhabitants, who are apparently largely of direct "Neolithic" descent without much intermixture with more "advanced" races, to have witnessed the effects of the occurrence (**7** *b*). Taking all the evidence into consideration the time of the final, and probably rapid, disappearance of the "lost lands" may be placed about the beginning of the second millennium B.C. or within the first quarter of that millennium, that is, at the close or soon after the close of the "Neolithic" Period in Britain.

Recent changes. After the close of the period of submergence the sea probably penetrated far up the present estuaries; but since then, owing to the accumulation of silt and the growth of vegetation, deposits of peat have been formed. The formation of storm beaches near the present outlets of the rivers, which seriously affects the drainage of the low-lying land bordering the estuaries, the deposition of silt on the valley floors a short distance above the present tidal limit, causing serious flooding, the cutting back of the heads of the streams into the plateau flats, and the formation of screes, alluvial fans, and lake deltas in the high zone, are the most conspicuous physical changes taking place at the present time.

Despite local changes in the superficial deposits of the coastal fringe giving the semblance of the sinking of the land there is no definite evidence of actual (appreciable) change in the relative levels of land and sea since the close of the period of the "Neolithic submergence[1]."

3. THE TRANSECT (*A, B, C*—Pl. I, Phot. 1 and Map 2).

Introduction. In this region of high relief the master factor determining the general distribution of the vegetation is altitude, and three main altitudinal zones are readily discernible: from the valley bottom to the upper limit of the "ffridd," marked by the uppermost line of wall stretching along the slope, is the zone of cultivation and rough enclosed pasture; at the highest level—on the high summits and for some distance down the steep slopes—is the zone of arctic-alpine vegetation; and in between them is the zone of moorland vegetation.

The present inhabitants, in general, live on the flats fringing the coast and in the valleys below the 600 ft. (183 m.) line; but the earliest settlers lived on the treeless uplands above this line and usually at not too great a distance from the sea. In prehistoric times the valley floors must have been swampy and covered with a tangled growth of vegetation, and for a considerable part of this period the valley slopes were thickly wooded far above the present limit of trees: the highest zone, then as now, was entirely inhospitable.

---

[1] On the other hand, "the more or less substantial tradition of the submergence of medieval and earlier villages off the coasts of Carmarthenshire, Cardiganshire and Caernarvonshire may indicate a continuation of the same process (i.e. the sinking tendency) down to more recent times" (**20**).
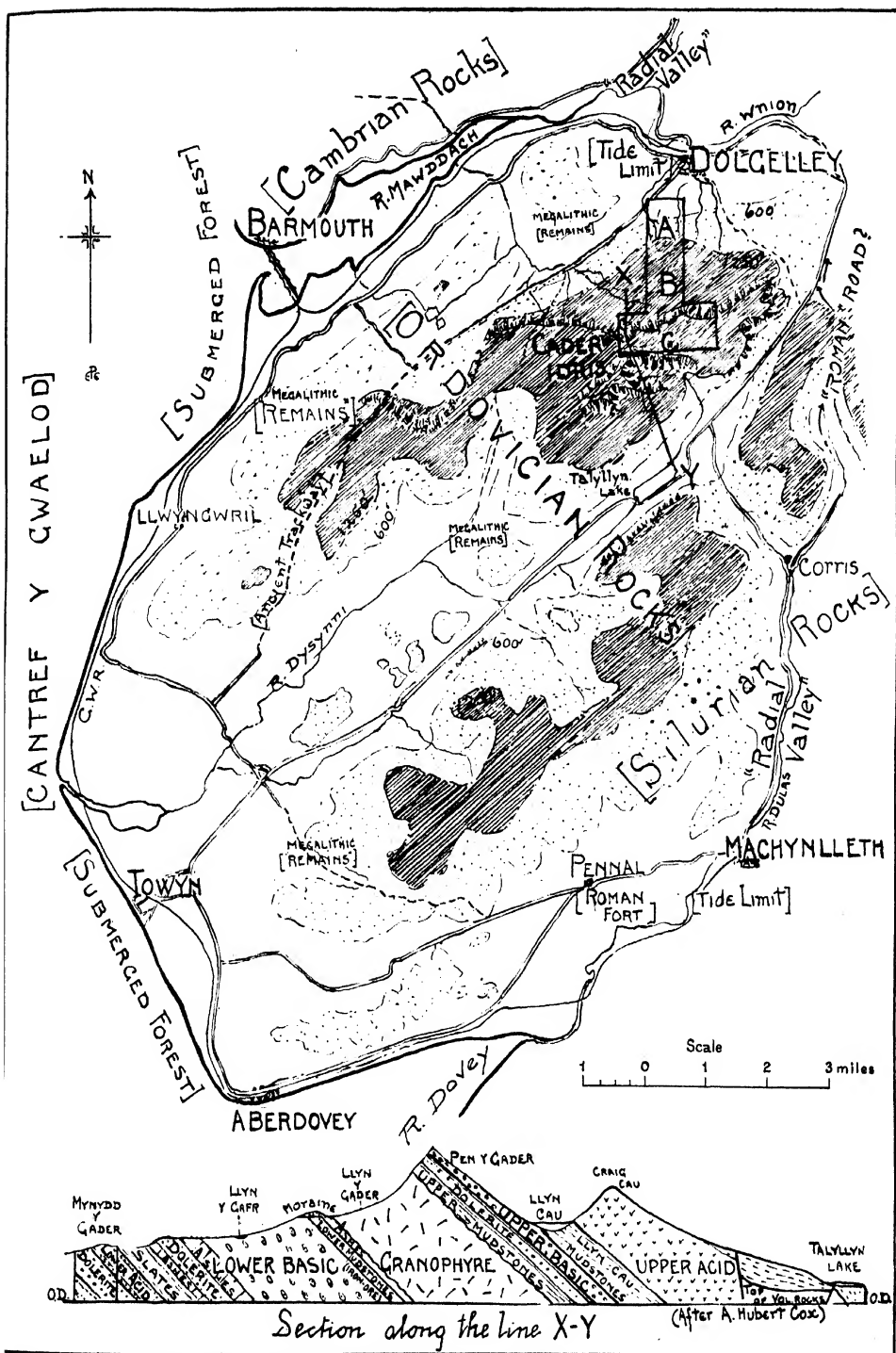
MAP 2. South-west Merioneth between the Mawddach and Dovey estuaries, showing the situation of Cader Idris and its geological structure (section), the transect, occurrence of Megalithic remains, etc.

Prehistoric man was thus largely confined by his geographical surroundings to a narrow strip near the coast. On the other hand, the presence of flint on the sea beach and the greater opportunity for hunting and fishing offered by the coastal swamps, combined with early man's predilection, by nature or by design, for upland regions, rendered the treeless uplands with good pasturage near the coast more suitable for settlement than any other region within the area. A study of the distribution of "remains" confirms this statement: they are to be found in the western part of the area on the uplands near the sea and generally on or near the course of the ancient trackways which traversed the district from north to south, from tide limit to tide limit, along a line more or less parallel to the coast-line (Map 2). They cannot claim to be of the highest antiquity, but some of them probably date from the "Neolithic Period" and certainly from the "Bronze Period[1]." To the north of the area at Tomen y Mur (Trawsfynydd) is the site of an old Roman fort and on its southern edge at Cefn-Caer (Pennal) (Map 2) are the remains of another Roman fort. Tradition has it that a "great" road (passing through the Cader area) joined these two places; but up to the present no definite trace of such a structure has been discovered. It is probable that this part of Wales and also that to the immediate south of the Dovey was never firmly held, at least directly, by the Romans[2]. Land communication between these "stations" was, probably, by means of the old pre-Roman trackways which followed the coast or more probably the line of the old "radial" valleys to the east[3] (Map 2). Apart from the natural degeneration which had set in at least as early as the beginning of the "Neolithic" Period, and the attack of domesticated animals, the forest suffered its first direct human attack during the "Bronze Period" and this attack has been continued intermittently ever since. The land thus reclaimed formed stretches of open country, though some of it may have been enclosed at the time of reclamation. It is certain that much enclosure took place during the period A.D. 1600–1700; but the great period of enclosure in Wales was the eighteenth and the first quarter of the nineteenth century. The close of this period saw the great policy of enclosure carried to completion. "The result of the enclosures was to cause a great change in the landscape of the land, and from this period date the great stone fences, so marked a feature of Merioneth....There is no doubt that their erection furnished much employment in the days of economic stress that followed upon the Napoleonic Wars[4]." To relieve the strain still further, trees were planted, and some of

---

[1] The "Neolithic" and "Bronze" Periods include the culture-periods Megalithic I and Megalithic II: note Megalithic Remains (Map 2).

[2] See *Gyda'r Wawr* edited by **H. J. Fleure** and published by Hughes and Son, Wrexham (1923).

[3] See "Roman Roads in Wales" by **H. E. Forrest** in *The North-Western Naturalist*, 4, No. 1, March 1929. This is an attempt to trace the course of this (supposed Roman) road from north to south through mid-Wales.

[4] *The Story of Two Parishes: Dolgelley and Llanelltyd* by **T. P. Ellis**, published by the Welsh Outlook Press, Newtown, Mont.

the plantations in this district date from that time. The study of the apportionment of the land between the respective farms on the northern flank of Cader Idris is instructive. Below the mountain wall the farms consist of radial strips bounded laterally by stone walls that follow the lines of the watercourses, and it is interesting to note, that the farm buildings in each case are situated near a watercourse and that the boundary walls cross and re-cross the streams at intervals in order to ensure the equitable division of potable water. Above the wall is the open grazing land (sheep walk) on which the sheep wander at will. There is an understanding but not a legal obligation concerning the number of sheep that a farmer may put on the open mountain[1], for, though unenclosed, theoretical boundaries between the lands belonging to the several farms are recognised. During the winter months (November to April) the sheep occupy the lowest zone and, in cases of insufficient grazing accommodation, the yearling ewe lambs are "wintered" on farms near the coast. This is an interesting case of transhumance.

The three accompanying sketch-maps (Maps 3, 4, 5—taken together) represent a belt transect up the north-facing slope of Cader Idris from the lower valley slopes to the summit plateau at right angles to the strike of the rocks. This belt comprises within itself a considerable part of the geological succession of Cader Idris, including two important intrusive sills, the four groups of volcanic, and considerable thicknesses of sedimentary rocks. Owing to the presence of alternate bands of hard and soft strata, the whole transect presents the appearance of a series of terraces and sloping steps giving a succession of wet and dry belts. In a district of high precipitation there is naturally a preponderance of peaty soil, acid in reaction: this is markedly so everywhere on the terrace flats and even on sloping ground in the high zone. In parts of the arable zone, however, there are deposits of "drift" or alluvium which give the characteristic soil known as stony loam, without a peaty covering.

A. *The zone of cultivation and rough enclosed pasture* (Map 3).

This zone embraces all the arable land, meadows, enclosed pastures of all grades, woodland and scrubland, and ranges from the valley bottom to the mountain wall. Though of no very constant height above sea-level this wall forms a distinct boundary of great utility to the sheep farmer and of some ecological significance: it occupies a place somewhere within the transition zone between lowland and moorland, usually above the tree line (c. 1100 ft.: 335 m.) and in general above the upper limit of bracken and gorse[2].

---

[1] The open mountain can carry about 3 sheep per 2 acres: the best "ffridds," 2 to 3 sheep per acre.

[2] On the north face of Cader Idris, within this transect, bracken ceases at the wall, very rarely crossing it, or at about 1350 ft. (411 m.) if the wall runs at a higher level. The wall acts as a barrier (or at least a hindrance) to the upward extension of this plant; but where there is

Arable land. The usual rotation on the upland sheep farm within this area is as follows: potatoes, barley, clover, oats, in the order given. Wheat rarely appears in the rotation and the growing of grain is of secondary importance in a sheep-farming district.

The following list of weeds of arable land on medium stony loam (av. $pH = 6.8$) is a summary of twenty-three observations (covering a period of four years) chiefly on fields belonging to Brynrhug at an altitude of 500–600 ft. (152–183 m.)[1].

(a) Percentage abundance above 50.

Name	No. of times seen (max. 23)	No. of times dominant or sub-dominant	% abundance*
Polygonum persicaria	20	11	67
Ranunculus repens	23	5	63
Galeopsis spp.	20	2	61
Rumex acetosella	20	9	58
Agrostis spp.	20	5	56
Brassica spp.	19	6	52

* The percentage abundance was calculated as in the following example:

Field record for *Agrostis* spp. = d. (2), s. (3), f. (12), o. (3), r. (0) according to scale of points d. = 5, s. = 4, f. = 3, o. = 2, r. = 1.

$$\text{Therefore points for } Agrostis = 10 + 12 + 36 + 6 + 0$$
$$= 64$$
$$\text{Maximum} = 23 \times 5 \text{ (23 observations)}$$
$$= 115$$
$$\text{Therefore \% abd.} = \frac{64 \times 100}{115} = 56.$$

d. = dominant, s. = sub-dominant, f. = frequent, o. = occasional, r. = rare.

These plants may be regarded as the six worst weeds within the area. *Brassica campestris* and *Sinapis arvensis* are included under *Brassica* spp.; *Galeopsis tetrahit* and *G. speciosa* under *Galeopsis* spp.

a fair depth of soil underneath the wall the underground stems are able to force their way to the other side and this is actually taking place at the present day in parts of the transect. It is not likely however that the plant will succeed in establishing itself, here, above the wall, owing to the vigilance of the farmer who nips off the tops of the shoots as they appear above ground; but to the immediate east of the area mapped, the plant has succeeded in passing under the wall and has spread into the moorland to a distance of about 15 yards from the wall.

Speaking generally the upper limit of *Ulex gallii*, of normal growth, is the same or slightly lower than that of bracken, but dwarf clumps may be found here and there on the moorland up to 1500 ft., and in one case a very dwarf clump was found near the top of Mynydd y Gader at about 1780 ft. (543 m.). *Ulex europaeus* is rather frequent in the lowland valleys but reaches its upper limit within the transect at about 600 ft. In the Central Uplands (Mid-Wales) "Bracken (*Pteris*) often ceases abruptly at about 1250 ft., while the mountain side continues of the same character far above its upper limit. The smaller Gorse (*Ulex gallii*) also is often seen to become dwarfed as the result of increasingly rigorous climatic conditions" (2). The top limit of bracken for the same area is given as 1500 ft. (457 m.). (19): on the southern slopes of Cader Idris (in Cwm Cau) it grows along the sides of a wall up to about 1600 ft. (488 m.).

[1] This is the limit of cultivation within this transect, but in the sheltered Aran Valley to the east it reaches 950 ft. (290 m.). In the Central Uplands to the south it reaches 1100 ft. (335 m.) (2).
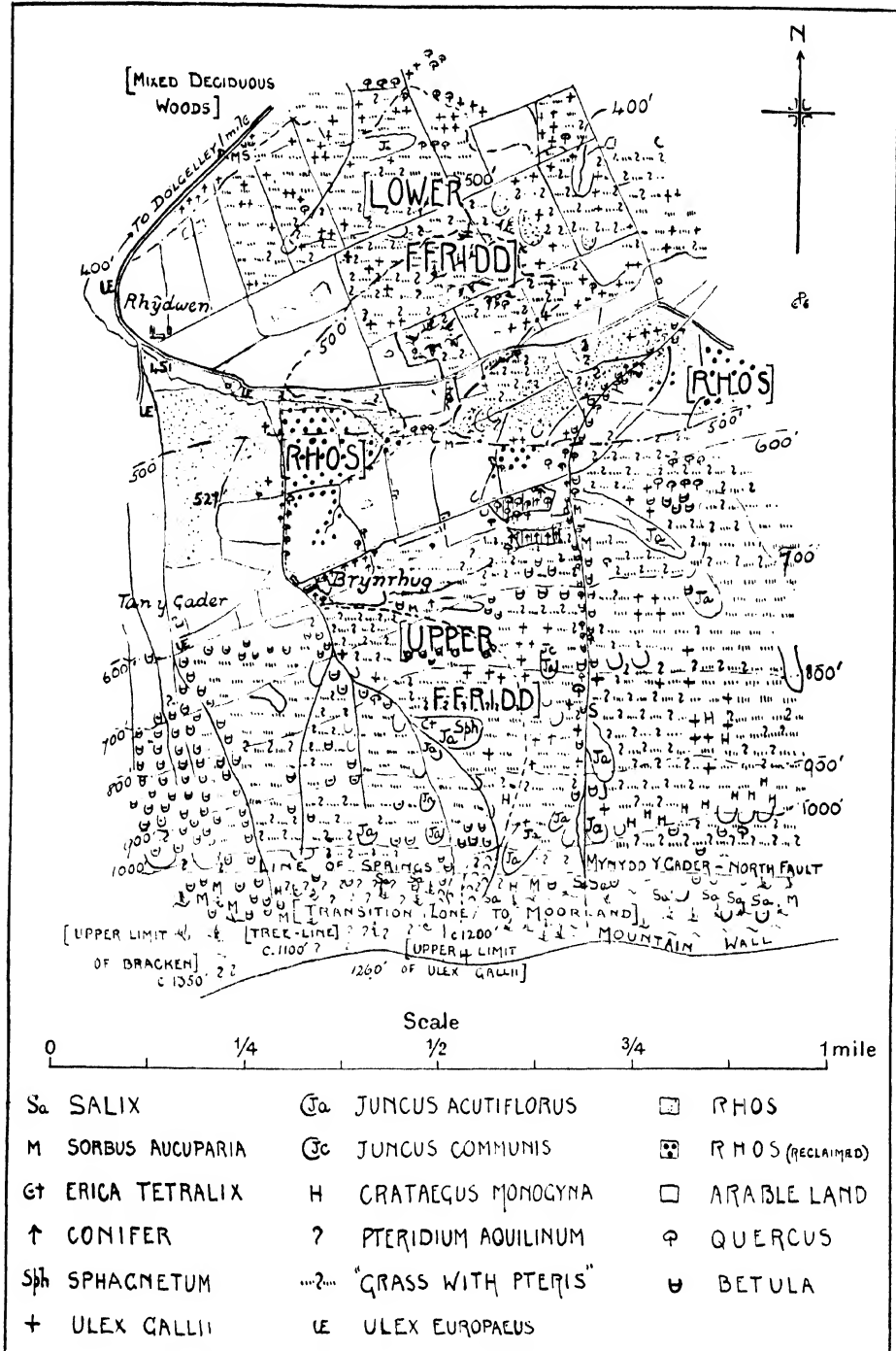
Map 3. Zone of cultivation and rough enclosed pasture (ffridd).

(b) *Percentage abundance between 50 and 25.*

Name	No. of times seen	No. of times dominant or sub-dominant	% abundance
Vicia cracca	21	0	48
Spergula spp.	22	1	45
Arrhenatherum bulbosum	20	0	43
Sonchus arvensis	18	0	40
Lotus sp.	21	0	39
Crepis virens	18	0	35
Holcus lanatus	17	2	34
Euphorbia helioscopia	16	0	31
Plantago lanceolata	15	1	30
Stellaria media	12	2	27
Polygonum convolvulus	14	0	26
Mentha arvensis	13	0	25

Spergula spp. include *S. sativa* and *S. arvensis*: out of 498 plants examined, 452 were *S. sativa* and 46 *S. arvensis*. This gives an approximate ratio of 9·8 : 1 in favour of *S. sativa* (cf. **9** a).

(c) *Percentage abundance under 25.*

Centaurea nigra	24	Alchemilla vulgaris	4
Cerastium vulgatum	24	Capsella bursa-pastoris	3
Hypochoeris radicata	24	Sagina procumbens	3
Achillea millefolium	23	Senecio jacobaea	3
Lathyrus pratensis	23	Stachys arvensis	3
Rumex acetosa	23	Trifolium sp.	3
Viola arvensis	23	Tussilago farfara	3
Bellis perennis	21	Veronica arvensis	3
Prunella vulgaris	20	Atriplex patula	2
Vicia sepium	19	Cardamine hirsuta	2
Achillea ptarmica	17	Centaurea scabiosa	2
Rumex obtusifolius	17	Cirsium lanceolatum	2
Stachys palustris	17	C. palustre	2
Polygonum aviculare	16	Filipendula ulmaria	2
Raphanus raphanistrum	14	Geranium molle	2
Leontodon autumnalis	13	Gnaphalium uliginosum	2
Poa annua	12	Heracleum sphondylium	2
Polygonum hydropiper	12	Hypericum dubium	2
Rumex crispus	12	Juncus bufonius	2
Veronica serpyllifolia	11	Lamium purpureum	2
Chrysanthemum leucanthemum	10	Linum catharticum	2
Cirsium arvense	10	Lythrum salicaria	2
Chrysanthemum segetum	9	Potentilla erecta	2
Myosotis arvensis	8	P. reptans	2
Polygonum lapathifolium	7	Rhinanthus crista-galli	2
Euphrasia officinalis	7	Senecio vulgaris	2
Fumaria sp.	7	Sherardia arvensis	2
Anagallis arvensis	5	Stellaria graminea	2
Plantago major	5		

The absence of *Papaver* spp. is noteworthy.

Meadows and associated pastures. Arable weeds are alien to their situation and are open plant communities: grassland weeds are native to the soil and with the rest of the herbage form closed communities. On arable land these plants are weeds under all circumstances: in meadows and pastures some of them are useful constituents of the herbage if not present in too great a quantity. A study of the herbage of meadows and pastures on medium stony loam at an elevation of about 600 ft. (183 m.) showed that, almost invariably, the dominant grasses were *Holcus lanatus, Agrostis* sp., *Cynosurus cristatus* and

Anthoxanthum odoratum: whatever the original seed mixture may have contained, after ten years the land had come under the complete dominance of these grasses, the first two of which must be regarded as weed grasses. The cause is largely attributable to faults in the prescription of the grasses to be sown. Experiments conducted (1922–8) under the direction of the Organiser in Agriculture for the County of Merioneth[1] have shown that, speaking generally, seed mixtures suitable for such land should contain *Lolium perenne*, *Dactylis glomerata* and *Phleum pratense*, with a proportion of the better class native grasses of fine bottom growth such as *Poa trivialis*, *Cynosurus cristatus* and *Anthoxanthum odoratum*, and in particular wild white clover.

Centaurea nigra, though possessing a certain feeding value, is far too common especially on the meadows, as also is *Heracleum sphondylium*. *Rhinanthus crista-galli*, which reduces the crop, is abundant on some of the pastures and *Linum catharticum*, which is positively injurious, is of too frequent occurrence.

Judging from the distribution of the remnants of former plant communities it seems that, before cultivation, these plateau flats at an elevation of 500–600 ft. (152–183 m.) consisted of woodland, scrubland or bogland. On "drift" soil, where the drainage was naturally good, sessile oakwood prevailed; on thin peat resting on "drift" deposits with slightly impeded drainage there was birch scrub with open patches dominated by *Molinia caerulea*, with *Myrica gale* and *Salix* spp. dominant along the watercourses; and on thick peat where the water was stagnant and acid there were Sphagnum bogs. At the present time the sessile oakwood has given way to arable land, meadow and pasture, on medium stony loam; but the bogs, though restricted in area, have remained much as they were owing to difficulties with respect to drainage. In between the arable land proper and the bogs there is a belt of land of considerable botanical interest and of some agricultural value. Such land, characterised by deficient drainage, by a thin surface layer of peat and by drainage water which is only moderately acid and not usually stagnant, is known as a "rhos"[2]—a term which conveys the idea of the peaty nature of the soil and implies the habitat of a distinctive kind of vegetation of rather low nutritive value. Within this transect and in the adjoining areas the "rhos" is a Molinietum caeruleae. On account of the difficulty of bringing it under cultivation this kind of land is often left to its own devices; on the other hand by firing, draining, manuring and liming, the best parts can be converted into moderately productive meadows, as has actually been done on the best farms (cf. **10, 9** *a*, **9** *b*).

The list on p. 16 gives the comparative frequency of the plants on (*a*) a typical "rhos" which has been mown regularly once a year for some years and which serves as pasture for cattle in winter, and (*b*) an unreclaimed portion of the same land.

---

[1] Merioneth Education Office, Dolgelley, North Wales: published in Welsh.

[2] Pronounced as spelled, with a long "o."

	(a)	(b)		(a)	(b)
Achillea ptarmica	r.	o.	Lotus spp.	o.	f.
Agrostis spp.	a.	o.	Luzula campestris forma		
Anemone nemorosa	l.	—	congesta Syme	o.	o.
Anthoxanthum odoratum	a.	f.	Menyanthes trifoliata	o.	l.a.
Bellis perennis	l.	—	Molinia caerulea	d.	d.—a.
Carex echinata	o.	f.	Myrica gale	—	l.a.
C. goodenowii	o.	l.a.	Nardus stricta	o.	o.
C. panicea	l.a.	o.	Narthecium ossifragum	o.	l.a.
C. pulicaris	—	o.	Orchis maculata	o.	o.
C. dioica	—	o.	Pedicularis palustris	a.	o.
Cardamine pratensis	—	o.	Pinguicula vulgaris	—	o.
Cerastium vulgatum	o.	—	Plantago lanceolata	l.a.	o.
Cirsium palustre	o.	o.—r.	Polygala vulgaris	o.—f.	o.
Dactylis glomerata	o.	—	Potentilla erecta	f.	f.
Drosera rotundifolia	o.	f.	Prunella vulgaris	o.—f.	—
Epilobium palustre	o.	o.	Ranunculus acris	o.	—
Erica tetralix	o.—f.	a.	R. repens	l.a.	o.
Eriophorum angustifolium	o.	f.	Rumex acetosa	f.	—
E. vaginatum	—	o.	Scabiosa succisa	o.—f.	f.
Euphrasia officinalis	f.	o. .	Scilla nutans	l.	—
Festuca ovina	a.—f.	o.	Scirpus caespitosus	l.a.	o.
Galium saxatile	o.	o.	Taraxacum vulgare	o.	—
Habenaria bifolia	r.	r.	Trifolium spp.	l.	—
Holcus lanatus	f.	o.	Triodia decumbens	o.	o.
Hydrocotyle vulgaris	l.a.	o.	Ulex gallii	—	o.
Hypochoeris radicata	o.	—	Vaccinium myrtillus	o.	o.
Juncus acutiflorus	o.	l.a.	Viola palustris	o.	o.
J. communis	o.	o.—f.	Hypnum spp.	f.	f.
J. squarrosus	o.	a.	Polytrichum commune	l.a.	o.
Leontodon autumnalis	f.	f.	Sphagnum sp.	l.a.	d.—a.

a = abundant, l = local.

The plants of the ditches, of which the most conspicuous are *Hypericum elodes*, *Filipendula ulmaria* (local), *Ranunculus flammula,* *Mimulus luteus* and *Dryopteris montana*, are not included in the above lists. (The water in the ditches has an average *p*H value of 6·2.)

Anemone nemorosa and *Scilla nutans* are present only near the edge, where the "rhos" passes into land on medium stony loam: these plants (and the tree stumps in the peat) are relics of a former woodland (Quercetum sessiliflorae). The soil consists of peat (*p*H 5·6) ranging from a few inches to about 2 ft. (61 cm.) in depth, resting on a subsoil of gravel or clay (*p*H 7·1). The vegetation of the cultivated "rhos" (*a*) resembles, in some respects, that of the adjacent meadow land on medium stony loam, but that of the unreclaimed "rhos" (*b*) approximates to that of the Sphagnum bogs. On these uplands (*c*. 400–600 ft.: 122–183 m.) the "rhos" lands (Molinieta caeruleae) are situated on the slopes between the well-drained slightly acid or neutral land on stony loam of the upper slopes, and the stagnant, acid and relatively deep, peaty deposits of the plateau flats: they are thus intermediate in character—in position, soil, drainage and vegetation—between neutral or slightly acid loamy land and acid bogland.

The rough enclosed hill pasture. Below the mountain wall all the land that is not under ordinary farm management or that is not woodland or scrubland is rough enclosed hill pasture or "ffridd[1]." Though often poor land on account

---
[1] Pronounced like "freathe" to rhyme with "breathe" (Eng.).

of its rocky nature, or its swampy condition, the "ffridd" plays a very important part in the economy of the upland sheep farm, and the amelioration of the herbage is claiming more and more of the attention of the farmer. Viewed as a whole it consists of grassland communities—generally a mixture of *Nardus* and *Molinia* grassland often with an abundance of dwarf *Scirpus caespitosus* and with facies where *Ulex gallii, Pteridium aquilinum, Festuca ovina,* and *Agrostis vulgaris* become locally dominant—and of swamp or moor communities which are Junceta, where the water is moving and is neutral or slightly acid, and Sphagneta or *Erica tetralix* bogs, where it is stagnant and acid.

The following is a representative list of species of the Upper Ffridd[1], omitting those on bare rock or on the banks of streams. The plants are classified here partly for the sake of convenience of description and partly for the purpose of bringing out certain features concerning habitats and the relative nutritive value of the herbage.

A = bogs.
B = swamps.
C = "Grass with Pteris."
D = gorse bosses.

E = *Nardus-Molinia* grassland.
F = recently cleared woodland.
G = area that has been limed.
H = land with good herbage ("Lager Platz," etc.).

	A	B	C	D	E	F	G	H
Achillea millefolium	—	—	o.	—	—	—	f.	f.
Agrostis alba	o.	o.	—	o.	a.—f.	—	—	—
A. vulgaris	—	—	d.	o.	o.	l.d.	l.d.	l.a.
Alchemilla vulgaris	—	—	—	—	—	—	—	o.
Anagallis tenella	—	o.	—	—	—	r.	—	—
Anthoxanthum odoratum	—	o.—f.	o.	—	—	f.	o.	o.
Athyrium filix-foemina	—	—	—	—	—	l.a.	—	—
Bellis perennis	—	—	—	—	—	—	o.	l.a.
Betula (seedlings)	—	—	—	—	—	o.—r.	—	—
Blechnum spicant	—	—	o.	—	—	o.—f.	—	—
Calluna vulgaris	o.—f.	o.	r.	f.	f.—a.	o.	r.	—
Campanula rotundifolia	—	—	o.	—	—	—	o.	—
Carex binervis	—	—	o.	f.	o.—f.	o.	o.	—
C. dioica	o.—r.	—	—	—	—	—	—	—
C. echinata	f.	o.	—	—	—	—	—	—
C. goodenowii	o.—f.	—	—	—	—	—	—	—
C. panicea	o.	o.	—	—	o.—f.	—	o.	o.
Cerastium vulgatum	—	—	r.	—	—	o.	o.	o.
Cirsium palustre	r.	o.—f.	—	—	—	r.	r.	r.
Conopodium denudatum	—	—	o.	—	—	—	—	—
Cynosurus cristatus	—	—	—	—	—	—	—	o.
Deschampsia flexuosa	—	—	o.	o.	—	l.d.	—	—
Digitalis purpurea	—	—	o.	—	—	o.	—	—
Drosera rotundifolia	f.	o.	—	—	—	—	—	—
Dryopteris dilatata	—	—	—	—	—	l.	—	—
D. filix-mas	—	—	—	—	—	l.	—	—
Empetrum nigrum	o.	—	—	—	—	—	—	—
Epilobium palustre	—	o.—f.	—	—	—	—	—	—
Erica cinerea	—	—	o.—r.	f.	o.—f.	—	—	—
E. tetralix	a.	f.	r.	f.	a.	—	—	—
Eriophorum angustifolium	l.a.	o.	—	—	—	—	—	—
E. vaginatum	l.a.	o.	—	—	—	—	—	—
Euphrasia officinalis	o.	—	—	—	—	—	—	—
Festuca ovina	o.—r.	o.—r.	f.—a.	o.	o.—f.	l.a.	f.—a.	l.a.
Galium saxatile	—	—	f.	o.—f.	o.	a.	f.	o.—f.

[1] The plants of the Lower Ffridd (c. 400–500 ft. : 122–152 m.) include vagabond species of hedges, road-sides, etc. and are not listed on this account.

	A	B	C	D	E	F	G	H
Hieracium pilosella	—	—	—	—	—	—	r.	o.
Holcus lanatus	o.	o.—f.	o.	—	—	o.	—	—
H. mollis	—	—	o.	—	—	o.	—	—
Hydrocotyle vulgaris	—	f.	—	—	—	—	—	—
Hypericum elodes	l.a.	—	—	—	—	—	—	—
Hypochoeris radicata	—	—	—	—	—	f.	—	—
Jasione montana	—	—	—	—	o.	—	—	o.
Juncus acutiflorus	o.	d.	—	—	—	—	—	—
J. communis	o.	l.d.	—	—	—	o.	r.	—
J. squarrosus	o.—f.	f.	—	—	f.	r.	—	—
Leontodon autumnalis	—	o.	r.	—	—	—	—	o.
Linum catharticum	—	—	—	—	—	—	—	o.—r.
Lotus corniculatus	—	a.	o.	—	—	o.—f.	o.	o.—f.
Luzula campestris	r.	—	r.	r.	—	—	o.	o.
Menyanthes trifoliata	l.a.	—	—	—	—	—	—	—
Molinia caerulea	f.	f.	f.	f.	c.d.	—	—	r.
Nardus stricta	o.	r.	o.	o.	c.d.	r.	o.	o.
Narthecium ossifragum	f.	o.	—	—	—	—	—	—
Orchis maculata	—	o.	o.	—	—	—	—	—
Oreopteris montana	—	o.	o.—f.	—	—	—	—	—
Oxalis acetosella	—	—	o.	—	—	o.	—	—
Pedicularis palustris	o.	—	—	—	o.	—	—	r.
Pinguicula vulgaris	o.	o.	—	—	—	—	—	—
Plantago lanceolata	—	—	—	—	—	—	o.	a.
Poa annua	—	—	—	—	—	o.	o.—f.	l.a.
Polygala vulgaris	o.	o.	o.	r.	o.	—	—	—
Potamogeton natans	l.	l.	—	—	—	—	—	—
Potentilla erecta	o.—f.	a.	a.	a.	f.	a.	o.—f.	o.—f.
Prunella vulgaris	—	o.	—	—	—	—	o.—f.	f.
Pteridium aquilinum	—	—	d.	o.	—	l.a.	—	—
Ranunculus acris	—	o.	r.	—	—	—	o.	f.
R. flammula	o.	f.	—	—	—	—	—	—
R. repens	—	—	o.	—	—	—	o.	o.
Rubus fruticosus	—	—	—	—	—	o.—f.	—	—
Rumex acetosa	—	—	f.	—	—	f.	—	—
R. acetosella	—	—	—	—	—	o.	o.	o.
Salix aurita	—	o.	—	—	—	—	—	—
S. capraea	r.	o.	r.	—	—	—	—	—
S. repens	—	r.	—	—	—	—	—	—
Scabiosa succisa	o.	f.—a.	—	—	—	—	—	—
Scilla nutans	—	—	o.	—	—	l.a.	—	—
Scirpus caespitosus	a.	o.	—	—	f.	—	—	—
Sorbus aucuparia (seedlings)	—	—	—	—	—	o.	—	—
Thymus serpyllum	—	—	—	—	—	—	—	o.
Trifolium repens	—	—	—	—	—	l.	l.a.	l.a.
Triodia decumbens	—	o.	—	o.	o.	—	o.	o.
Ulex gallii	—	—	o.	d.	f.—a.	o.—f.	—	—
Vaccinium myrtillus	o.—f.	—	o.—f.	o.	a.	o.—f.	—	—
Viola canina	—	—	o.	—	—	—	—	—
V. palustris	—	f.	—	—	—	—	—	—
Sphagnum spp.	d.	l.a.	—	—	—	—	—	—

Mosses are generally distributed in the grasslands and species of *Hypnum* are particularly abundant: patches of *Leucobryum glaucum* are conspicuous in the *Nardus-Molinia* grassland.

The bogs (*A*) are small patches generally dominated by *Sphagnum* sp. and locally by *Erica tetralix*, occupying stagnant hollows (which may be natural depressions or artificial hollows due to the removal of peat) in the plateau flats; the swamps (*B*) are more extensive areas generally dominated by *Juncus acutiflorus* and locally by *J. communis*, occupying the slopes in the neighbour-

hood of springs or flushes where the water is in motion. In the bogs *Scirpus caespitosus* and *Festuca ovina* (when it occurs) tend to be viviparous. "Grass with *Pteris*" (C) covers a considerable portion of the ffridd on the site of former woodland. *Pteridium aquilinum* is rarely attacked by animals (though horses have been observed to eat it) and though mown annually for litter it is probably spreading. The "ridge and furrow" on parts of the "ffridd" (800–900 ft.: 244–274 m.) shows that, in parts, the upper limit of cultivation is lower to-day than formerly—a fact that may be accounted for by changed economic conditions, as also may the present tendency to put more land under grass. The land thus thrown out of cultivation is often quickly overrun by bracken.

The *Ulex gallii* area (D) is occupied by small rounded bosses (1 to 4 ft. or 30 to 122 cm. in diameter and about 18 in. or 46 cm. high) of the gorse separated by small patches of grassland. On account of the mixed character of this area only plants actually growing on the bosses are listed. The roundness of the bosses is at least partly attributable to the grazing of sheep. The gorse is fired periodically, and though burnt areas may be invaded by such annuals (or biennials) as *Cirsium palustre* or *C. lanceolata* the ultimate effect is the improvement of the land and the development of small patches of grassland usually dominated by *Agrostis vulgaris*.

The *Nardus-Molinia* grassland (E) covers large areas of the Upper Ffridd, particularly where the ground is wet and peaty. As pasture land it is relatively poor, providing herbage which is largely unpalatable. The plants, particularly *Calluna, Ulex, Scirpus* and *Vaccinium*, are usually of a very dwarf habit—a condition which is induced by burning and to some extent by grazing. The recently cleared woodland (F) is in a transition stage between woodland and "Grass with *Pteris*": *Scilla nutans* still persists in fair quantity locally, and *Pteridium aquilinum* is spreading.

Now and again small quantities of lime are spread on selected areas of the "ffridd" with good results. These small areas (G) and those named "H" are the most productive on the "ffridd." The drainage of these parts is good and peat does not accumulate. It is interesting to note that many of them (H) occur round and about hawthorn shrubs which are remnants of the undergrowth of the old birchwood. Sheep are attracted to these parts for shelter and the habitat is improved as a result of high manuring.

The woodlands. Within this transect the nearest approach to virgin woodland is to be found on the slopes of the Upper Ffridd between 800 and 1100 ft. (244 to 335 m.). These birchwoods and the individual birch trees, dotted here and there in the pasture land and near the streams, are remnants of an old woodland that once probably covered the whole or most of this zone. Below the birch zone it is almost certain that no virgin forest exists, though the small areas of pure oakwood and the individual oak trees that remain here and there, may be regarded as representative of the woodlands that once

covered much of the slopes up to about 800 ft. (244 m.). In the lower parts of this oak zone it is certain that some of the oak trees and it is probable that all the conifers (see Discussion, p. 44) have been planted; but it is difficult to distinguish natural from artificial oakwoods in an area where the oak naturally dominates. Speaking generally it may be said that, where *Quercus pedunculata* is dominant and where the woodland is mixed deciduous or coniferous, planting has taken place; where the woodland is more or less pure sessile oakwood (Quercetum sessiliflorae) it is probably a remnant of the original forest. In the following table:

A represents the flora of a very small sessile oakwood at an elevation of 600 ft. (183 m.) on land that is grazed by cattle and sheep;

B the flora of a larchwood (Laricetum deciduae) planted about 25 years ago, at an elevation of 650 ft. (198 m.);

C the flora of a birchwood at an elevation of 800 to 1100 ft. (244 to 335 m.).

	A	B	C		A	B	C
Agrostis spp.	a.—d.	l.d.	d.	Larix decidua	—	d.	—
Anemone nemorosa	o.	—	—	Lonicera periclymenum	—	r.	—
Anthoxanthum odoratum	o.—f.	o.	f.	Luzula campestris *forma*			
Athyrium filix-foemina	o.	o.	o	congesta Syme	f.—o.	—	r.
Betula (hybrid spp.)	o.	—	d.	Melampyrum pratense	f.	—	—
Blechnum spicant	f.	—	o.—f.	Nepeta hederacea	—	l.	—
Calluna vulgaris	—	r.	r.	Oxalis acetosella	f.	f.—a.	a.
Cerastium vulgatum	r.	r.	—	Oreopteris montana	o.	—	f.
Circaea lutetiana	—	l.	—	Phegopteris polypodioides	—	l.	—
Conopodium denudatum	o.	—	r.	Potentilla erecta	a.	—	a.
Crataegus monogyna	—.	—	o.	Pteridium aquilinum	l.a.	o.	a.
Dactylis glomerata	o.	r.	o.—f.	Quercus sessiliflora and			
Deschampsia caespitosa	—	r.	—	hybrids	d.	—	r.
D. flexuosa	a.—d.	l.d.	f.	Rumex acetosa	r.	r.	—
Digitalis purpurea	o.	f.	—	R. acetosella	—	r.	—
Dryopteris dilatata	l.a.	f.	o.	Ranunculus repens	—	l.	—
D. filix-mas	o.	o.	o.	Rubus fruticosus	o.	o.	—
Festuca ovina	a.	o.	o.—f.	Rubus idaeus	o.	o.	—
Fraxinus excelsior	r.	r.	r.	Salix capraea	—	—	o.
Galium saxatile	a.	a.	a.	Scilla nutans	f.	o.—r.	r.
Geranium robertianum	—	l.	—	Sorbus aucuparia and			
Hedera helix	—	o.—r.	o.	seedlings	o.	o.—r.	o.—f.
Hieracium sp.	o.	—	—	Stachys sylvatica	—	l.	—
Holcus lanatus	o.	o.	o.	Triodia decumbens	o.	—	o.
H. mollis	f.—o.	f.	—	Viola canina	o.	—	o.
Hypericum dubium	—	r.	—	Vaccinium myrtillus	o.—f.	o.	f.
Hypochoeris radicata	o.	o.	—				

In all three woods the soil is shallow, rather dark, and moderately acid (the surface soil in the oakwood has a *p*H value of 5·8). The dominant species in the oakwood (*A*) is *Quercus sessiliflora*, but hybrid forms, *Q. sessiliflora* × *robur* (*pedunculata*), are present as in other parts of the district. One or two individuals of each of the following: *Pinus sylvestris, Ilex aquifolium, Acer pseudoplatanus, Fraxinus excelsior* occur, but they have no effect on the consociation as a whole. The absence of undergrowth (*Corylus avellana*, for instance, is usually abundant in other parts of the area) is due probably to heavy grazing. The larchwood (*B*) is a pure consociation excepting one or two self-sown ash trees. Species of *Boletus* are frequent on the ground in this wood. The birch-

wood (*C*) consists of hybrids between *B. alba* (*verrucosa*) and *B. pubescens*: a tree which is typical of either *B. verrucosa* or *B. pubescens* is difficult to find in this woodland or on the "ffridd" in general.

In all these woodlands mosses play a very important part in the composition of the ground flora and in places they are fully dominant. The following are abundant or frequent: *Hylocomium triquetrum, Thuidium tamariscinum, Plagiothecium undulatum, Dicranum scoparium, Hypnum* sp., *Mnium hornum, Polytrichum commune* and *Sphagnum* sp. *Cladonia* sp. is frequent locally amongst the ground flora of the oakwood. The trunks of the trees (excepting larch) are often covered with mosses and lichens, in particular on the windward side. In the oakwood the most conspicuous moss is *Eurhynchium myosuroides* which covers the base of the trunks of the trees and often ascends to the upper parts: *Usnea florida, Evernia prunastri* and *Cetraria glauca* are abundant lichens—*Usnea florida* in particular ascending to the crowns in increasing abundance with the ascent. *Polypodium vulgare* grows as an epiphyte in the moss on the trunks of the trees in the gorges cut by the streams.

B. *The moorland zone* (Map 4).

The moorland zone comprises the rough rock terrace of Mynydd y Gader and the Upland Valley between it and the main Cader escarpment: the rock terrace is a sill of dolerite overlain by lower acid volcanic rocks; the Upland Valley is a depression in the lower basic rocks. Minor intrusions also of dolerite occur here and there, but the slaty strata which normally occur in the succession elsewhere are only sparingly present here; they have thinned out or have been cut off by a series of normal faults which in the main follow the line of the Mynydd y Gader south fault. On the north face of Mynydd y Gader, at the base of the sill, is the north fault which separates the dolerite from the Upper Cambrian rocks underlying the Upper Ffridd. This fault line which is marked by a band of springs and flushes (Maps 3 and 4) is the ecological boundary[1] between the moorland and the lowland.

After allowing for the effect of altitude it may be said that the factor determining the nature of the plant covering in general is the drainage. On the flat or gently sloping summits of Mynydd y Gader and on the divide across the Upland Valley near Craig y Bwlch, where the drainage is very defective, there are small areas of wet moor of a mixed character but mainly cotton-sedge moor; on the upper slopes, where the drainage is better, is the grass moor, in which *Nardus stricta* is usually fully dominant; and on the still better-drained lower slopes there are patches of heather moor in which *Calluna vulgaris* is supreme. Eriophoreta, Nardeta and Calluneta are the chief moor communities here and they give the impress to the vegetation as a whole.

---

[1] The mountain-wall, which is the economic boundary, may not exactly coincide with the ecological boundary: the wall was built where the topographical features were best adapted for its construction.

MAP 4. Moorland Zone.

NARDETUM
◇ n   NARDUS STRICTA
Gt   ERICA TETRALIX
Js   JUNCUS SQUARROSUS

ERIOPHORETUM
(SPHAGNO-ERIOPHORETUM)

JUNCETUM
U Jc   JUNCUS COMMUNIS
Ja   JUNCUS ACUTIFLORUS

CALLUNETUM
/ 6   CALLUNA VULGARIS
M   SORBUS AUCUPARIA
H   CRATAEGUS MONOGYNA
Sa   SALIX
b   BETULA
+   ULEX GALLII
∞   ERRATICS

Scale ¼
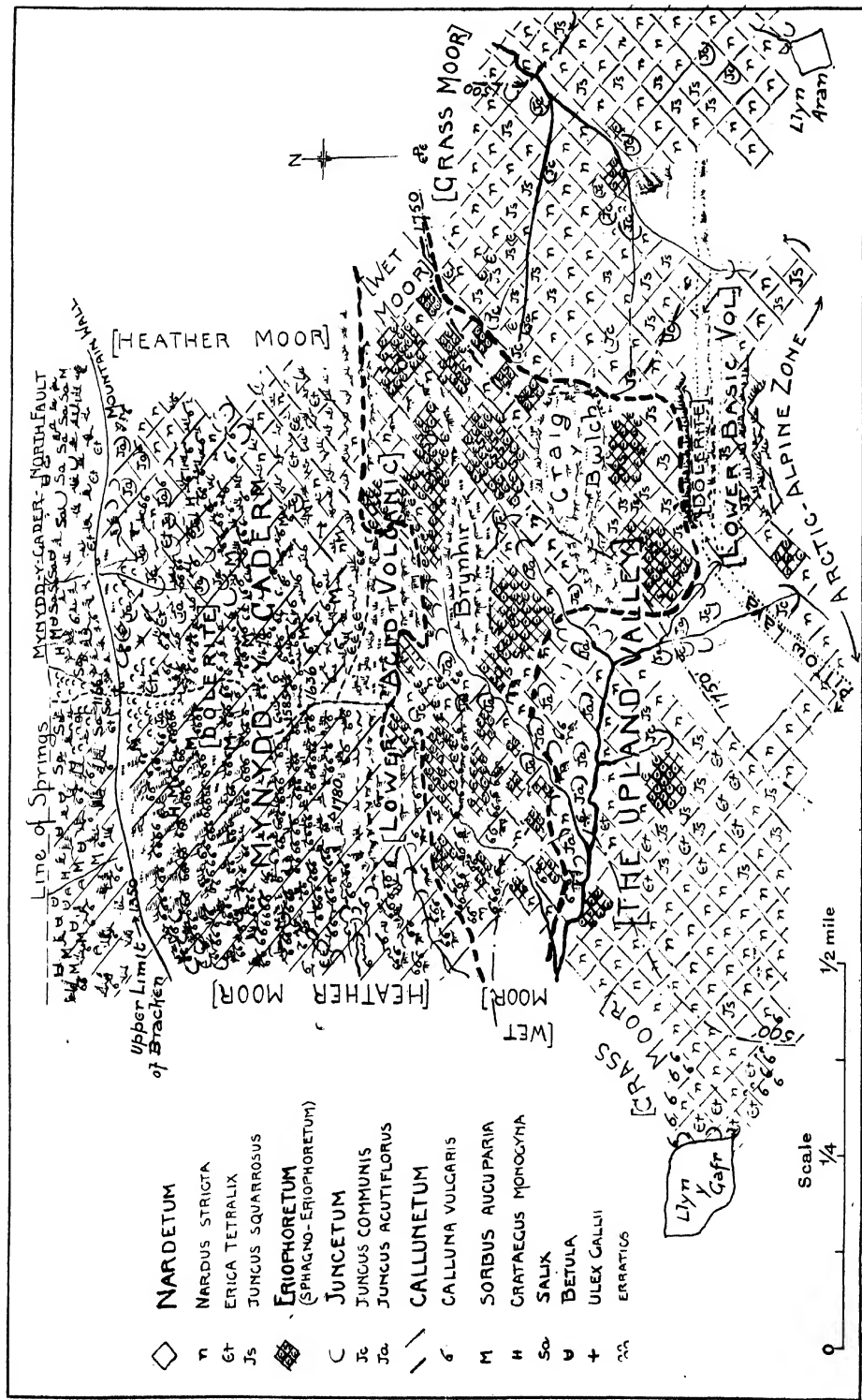
0   ½ mile

The wet moor. Characteristic features of the land at or about the summit of Mynydd y Gader are the flat or gently sloping peaty plateaux usually containing moor pools. As already stated the plant communities here may be described, in general, as Eriophoreta, but in reality they are mixed bogs in which wet-moor communities occur in concentric zones about the pool. The small pool[1] with its sparse phanerogamic flora, consisting of such plants as *Eriophorum angustifolium, Juncus supinus, Carex echinata, Scirpus fluitans,* and occasionally *Narthecium ossifragum,* but with an abundance of moss which is usually some species of *Sphagnum,* is surrounded by a community in which *Eriophorum angustifolium* and *Sphagnum* spp. are co-dominant. This Sphagno-Eriophoretum frequently contains small societies of *Scirpus caespitosus.* With decreasing water content this mixed community passes gradually outwards into one in which *Eriophorum vaginatum* is dominant and *Polytrichum commune* frequent. As the periphery is approached the dominant plants of the inner zones become less frequent and with the increasing abundance of such plants as *Juncus squarrosus, Erica tetralix, Calluna vulgaris, Vaccinium myrtillus, Nardus stricta,* and *Rhacomitrium lanuginosum, Cladonia* sp. and *Festuca ovina* (near the rocks), the wet moor finally passes into the Nardetum of the Upland Valley.

In late summer or early autumn these patches of wet moor present an interesting study in colour—the rusty red of the Eriophoreta angustifolii with the yellow-brown of the Scirpeta passing gradually into the light green of the Eriophoreta vaginati, into the darker green of the communities dominated by *Juncus squarrosus* and *Erica tetralix* and finally fading into the light grey of the Nardetum, the dominant colour of the moorland at this time of the year. These colour differences serve to distinguish the various groups of communities of the wet moor, and the dark grey of the bounding rocks serves further to emphasise the colour difference between wet moor and grass moor (cf. **11**).

Though *Eriophorum angustifolium* is often the dominant plant, yet typical Eriophoreta angustifolii are difficult to find. The nearest approach to a pure community is a small moor (Pl. III, Phot. 3) near the divide across the Upland Valley (*c.* 1750 ft.: 533 m.). It is constituted somewhat as follows:

Eriophorum angustifolium	d.	Agrostis alba	o.
Sphagnum sp.	s.	Carex rostrata	o.
Erica tetralix	a.	C. panicea	o.
Scirpus caespitosus	l.a.	Deschampsia flexuosa	o.
Carex echinata	a.—f.	Empetrum nigrum	o.
Drosera rotundifolia	f.	Pinguicula vulgaris	o.
Galium saxatile	f.	Polygala vulgaris	o.
Potentilla erecta	f.	Triodia decumbens	o.
Eriophorum vaginatum	f.—o.	Carex binervis	o.—r.
Calluna vulgaris	f.—o.	Calluna vulgaris *forma*	
Juncus squarrosus	f.—o.	albiflora	r.
Narthecium ossifragum	f.—o.	Equisetum limosum	r.
Polytrichum commune	f.—o.	Juncus communis	r.
Nardus stricta	f.—o.	Viola palustris	r.

[1] There may be several small pools on one plateau: in this case the concentric zones merge into one another on the periphery of each group. Where there are no moor pools there is no zonation: the wet-moor communities alternate with one another according to the water-content of the bog.

In the majority of cases the moor pools are small, the water is of aerial origin and moderately acid in reaction (*p*H 5·9), and the flora is very scanty; but in a few cases larger pools occur in large depressions and as the water is partly telluric and rather less acid (*p*H 6·2) there is present a somewhat richer flora.

The characteristic plants of two such pools at or near the summit of Mynydd y Gader (*c*. 1750 ft.: 533 m.) are as follows: *Utricularia minor* (a.), *Carex echinata* (a.), *Nitella flexilis* (a.), *Sphagnum* spp. (a.), *Carex rostrata* (l.a.), *Sparganium affine* (f.), *Scirpus fluitans* (f.), *Menyanthes trifoliata* (f.), *Equisetum limosum* (f.), *Narthecium ossifragum* (f.), *Ranunculus flammula* (o.), *Potamogeton polygonifolius* (o.), *Viola palustris*. *Sphagnum* spp. include *S. cymbifolium*, *S. papillosum*, *S. aquatile* and *S. obesum*. Pure communities of *Carex rostrata* may be found in one of the pools and similar communities occur here and there, chiefly near the watercourses of the upper slopes of the moorland.

It seems that the flora of these larger pools is intermediate in character between that of the small pools of acid water and that of the tarns (Llyn y Gafr and Llyn Aran) of neutral or slightly acid water.

It is interesting to note that buried wood may be found in the peat of some of these bogs and in that of the grass moor, up to an elevation of at least 1750 ft. (533 m.) (Plate III, Phot. 4). At or near the summit of the dip slope to the south and south-east of Llyn Aran there is a series of small plateau flats descending in step formation from the top of the ridge (*c*. 2200 ft.: 671 m.) to about 2000 ft. (610 m.) within the limits of this transect. As plant habitats these flats resemble those already described, but owing to their higher level and relatively better drainage they differ from them in important particulars. In general the plant communities may be described as Eriophoreta vaginati from the dominant community, but here again the communities are rather mixed: such plants as *Scirpus caespitosus*, *Juncus squarrosus*, *Polytrichum commune* (in bosses) and, near the small and infrequent pools, *Eriophorum angustifolium* and *Sphagnum* may assume local dominance. Notable features of these high wet moors are: the abundance of *Vaccinium myrtillus* mixed with rather stunted *Calluna* and the rarity or absence of *Erica tetralix*. The last-mentioned plant, abundant at 1750 ft. (534 m.), is rather scarce at 2000 ft. (610 m.) and appears to cease altogether a little above this level.

At this elevation (*c*. 2000 to 2200 ft.: 610 to 671 m.) the peat, which in places reaches a depth of 4 to 5 ft. (122 to 152 cm.), shows no trace of buried wood.

The highest wet moor within this transect, however, occurs in a small depression not far from the summit of Mynydd Moel at about 2700 ft. (823 m.). It differs from the normal wet moors at lower elevations in the greater abundance of *Juncus squarrosus*, the sparsity and extreme dwarfness of *Calluna vulgaris*, the absence of *Erica tetralix* and the greater abundance of mosses such as *Rhacomitrium lanuginosum* (growing in bosses on which *Cetraria*

Phot. 3. View of Sphagno-Eriophoretum (c. 1750 ft.: 533 m.) with moor pool Brynhir to left, summit of Mynydd y Gader to the right. Remains of buried wood may be found in this bog.
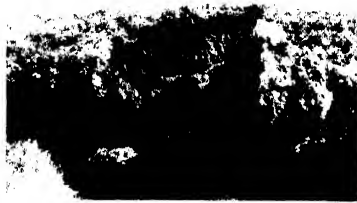
Phot. 4. Pool showing degeneration of peat. Buried wood (chiefly twigs) consisting mainly of species of *Betula* and *Salix* may be found near the base (under the stick). Altitude about 1750 ft. (533 m.).
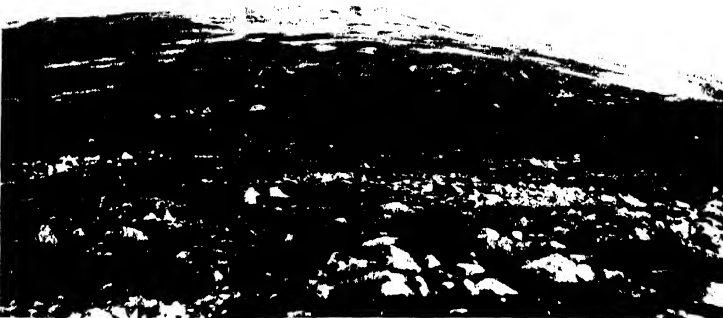
Phot. 5. View of summit of Mynydd Moel looking east. Moss lichen open association in distance and in foreground; *Rhacomitrium-Cladonia* heath and *Rhacomitrium* heath in between.

EVANS—CADER IDRIS: A STUDY OF CERTAIN PLANT COMMUNITIES IN SOUTH-WEST MERIONETHSHIRE

islandica is often "abundant"), *Hylocomium loreum* and *Hypnum schreberi*. An additional difference is the frequency of communities of *Luzula maxima* and the presence of *Festuca ovina* forma *vivipara*[1].

The cryptogamic flora of the small pool (pH 4·7), in this wet moor, includes *Hypnum fluitans, H. exannulatum, Sphagnum obesum, Chroococcus turgidus, ·Euglena acus, Binuclearia tatrana, Mougeotia* sp. and *Scytonema* sp.

These high-level wet moors (above 2000 ft.: 610 m.) may be regarded as examples of particularly elevated subalpine moorland associations within the arctic-alpine zone (see *Types of British Vegetation*, p. 315).

The grass moor. Within the limits of this transect the total area covered by wet moor is relatively small: with improved drainage the wet-moor communities pass almost imperceptibly into the grass moor which covers most of the Upland Valley. The soil is almost everywhere of a peaty nature and in some parts there are deposits of thick peat. The following list will give a general idea of the composition of the Nardetum and the relative frequency of its constituent species[2] (*c.* 1500–1800 ft.: 457–549 m.).

Nardus stricta	d.	Lycopodium alpinum	o.
Galium saxatile	a.	L. clavatum	o.
Juncus squarrosus	l.a.	Luzula campestris	o.
Erica tetralix	l.a.	Anthoxanthum odoratum	o.
Vaccinium myrtillus	a.—f.	Triodia decumbens	o.
Potentilla erecta	f.	Agrostis vulgaris	o.
Empetrum nigrum	f.	Cirsium lanceolatum	r.
Festuca ovina	o.—f. (l.a.)	Rhacomitrium lanuginosum	f.
Lycopodium selago	o.—f.	Hypnum schreberi	f.
Deschampsia flexuosa	o.—f.	Polytrichum commune	o.—f.
Polygala vulgaris	o.	Sphagnum sp.	o.
Carex binervis	o.	Cladonia sylvatica	o.—f.
C. panicea	o.	C. uncialis	o.

The grass moor just described may, in places, pass into the high-level (or "arctic-alpine") grassland at as low an altitude as 1500 ft. (457 m.); but normally the change takes place between 1800 and 2000 ft. (549–610 m.). On the summit plateau, however, a modified grass moor—an elevated grass moor within the arctic-alpine zone—may be found up to 2700 ft. (823 m.). In this elevated grass moor *Nardus stricta* is still dominant, but *Juncus squarrosus* and *Festuca ovina* are locally abundant, and, in places where peat (depth 1 to 2 ft.: 30 to 61 cm.) has accumulated, small pure societies of *Luzula maxima* are frequent.

The heather moor (*c.* 1200–1700 ft.: 366–518 m.). The dolerite mass of Mynydd y Gader resembles the granophyre mass of the great escarpment in the poverty of its flora in comparison with that of the basic volcanic rocks; but it differs from it ecologically in its position at a lower level and in its more even and less precipitous surface. Despite the absence of a rich flora this zone is not without interest, and this lies chiefly in the variety of its plant habitats.

[1] This plant, however, was found occasionally in bogs as low as 800 ft. or 244 m.

[2] It will be noticed that *Molinia caerulea* does not appear in this list: it is not a constituent member of the Nardetum though it grows on the peat which has collected at the top of the boulders within the Nardetum.

The eastern side of the north-facing slope is composed chiefly of bogs, swamps, and patches of grass moor; the western side consists of patches of heather interspersed with bogs and swamps on the south-facing slope and with small areas of grassland on its north-facing slope; but a considerable portion of its surface is made up of "bare" rock—either vertical rock faces or loose boulders which are of scree formation or (in the lower parts) are local erratics.

With decreasing altitude the bogs of the summit, already described, give place largely to *Erica tetralix* bogs, and the swamps dominated by *Juncus communis* pass into those dominated by *Juncus acutiflorus* (see later, p. 29).

The patches of heather on the well-drained slopes of the western part of the north-facing slope afford the best example of a Callunetum within the transect; but the scarp slopes of Cader Idris in general are too rocky or precipitous to allow of the development of a continuous area of heather[1], and the nearest approach to typical Calluneta occurs on the more even dip slopes to the south of the area described in this paper.

Calluna vulgaris is locally dominant and *C. vulgaris* forma *albiflora* is sparingly present. Closely associated with *Calluna* are: *Erica cinerea*[2], *E. tetralix*[2], *Empetrum nigrum*, *Vaccinium myrtillus*, *Potentilla erecta*, *Galium saxatile*, and *Blechnum spicant*. Between the numerous boulders such mosses as *Rhacomitrium lanuginosum*, *Polytrichum commune*, *Plagiothecium undulatum*, *Hypnum* sp. and *Sphagnum* sp. are abundant and their decayed parts form the soil in which the heather grows. In addition to *Blechnum spicant*, *Dryopteris dilatata*, *D. filix-mas*, *Phegopteris polypodioides* and, very occasionally, *Cryptogramme crispa*, may be found in the hollows between the boulders.

In parts where finer material has collected between the rocks, and where the soil is rather dry, patches of grassland occur in which *Festuca ovina* and *Agrostis vulgaris* are locally dominant, with such plants as *Thymus serpyllum*, *Cerastium vulgatum*, *Oxalis acetosella*, *Potentilla erecta*, *Galium saxatile*, *Sedum anglicum* and *Digitalis purpurea* as associated species; on the sides of the small watercourses *Cirsium palustre*, *Filipendula ulmaria*, *Geum rivale*, and *Alchemilla alpestris* are frequent; and in places where the water is stagnant, especially on the eastern half of the rock terrace, patches of *Nardus* moor with *Juncus squarrosus* are common.

The prevailing colour of this rock terrace is grey—dark grey rocks covered with light grey lichens. In winter the scene is rather dismal; but in late summer or early autumn when the grass is fading but the heather still blooming the rock terrace is notable for the beauty of its colouring. The most abundant or characteristic lichens on the loose boulders of dolerite (c. 1200–1600 ft.: 366–488 m.) are species of the genus *Pertusaria*[3] of which the most notable is

---

[1] The heather on these slopes is fired periodically.

[2] Forms with pure white flowers are present, though rare.

[3] The dominant species of *Pertusaria* on these dolerite boulders is *P. dealbata*, but *P. lactea*, *P. sulphurea* and *P. concreta* forma *Westringii* are also more or less frequent.

the rare lichen *Pertusaria monogona*, for which "Cader Idris" (up to the present) is the only British record (*B.M. Monograph*). It is very interesting to note that, in addition to the *warted* form (already recorded), the rarer, somewhat *plane areolate* form of this lichen is also present. Both forms occur in good quantity, sometimes on the same boulder, but the plane areolate form seems to be the more abundant in this locality. (The reverse seems to be true of the relative frequency of the two forms on the Continent.)

Other conspicuous lichens and mosses here are: *Lecidea contigua* (f.) and forma *flavicunda* (f.—a.), *L. dicksonii* (f.), *Haematomma ventosum* (o.), *Rhizocarpon geographicum* (o.), *Parmelia omphalodes* (f.), *Stereocaulon evolutum* (f.), *Sphaerophorus globosus* (o.), *Cladonia cervicornis* (f.), *Lecanora gelida* (o.), *Rhacomitrium sudeticum* (o.) and *Andreaea petrophila* (o.—f.).

A few rather stunted individuals of *Sorbus aucuparia* and one or two of *Crataegus monogyna* may be found rooted in the cracks in the vertical rock faces. It is probable that the northern face of Mynydd y Gader was never thickly wooded owing to the rocky nature of the ground. The rowan and hawthorn are frequent at the present upper limit of trees and it is probable that those on the rock faces are invaders from the tree zone below rather than remnants of an old woodland: they have sprung from seeds carried by birds and dropped into rock fissures out of the reach of sheep. Another invader, this time from the arctic-alpine zone, is *Festuca ovina* forma *vivipara*, which may be found growing in the pockets of peat on the rocks.

Towards the summit of Mynydd y Gader the dolerite is replaced by lower acid volcanic rocks interspersed with small dolerite intrusions. Most of the lichens enumerated above are absent or only sparingly present on the acid volcanic rocks, which are closer grained than the dolerite and are less favourable as lichen habitats. On the side facing the south-west winds these rocks are often quite bare, though the lichen *Rhizocarpon geographicum* often stands out prominently on the creamy white surface which usually results from the weathering of rhyolitic rocks. The other side is darker—a condition which is intensified by the presence of lichens with a dark thallus such as *Lecidea rivulosa*, *L. kochiana* and *L. lygaea*.

There is an obvious difference between the vegetation of the summit of Mynydd y Gader and that of the lower slopes. The change in the bogs and swamps has been mentioned already; but the difference in altitude is also reflected in other forms of plant communities. *Calluna vulgaris* reaches its optimum between 1100 and 1600 ft. (335–488 m.): above this limit it is less abundant and rather dwarf. The small areas of grassland and the plants of the watercourses described above are characteristic of the lower slopes, and with increasing altitude they give place to vegetation that tends to be arctic-alpine in character. With increased elevation *Empetrum nigrum*, *Vaccinium myrtillus*, *Festuca ovina* forma *vivipara* become more abundant. *Lycopodium alpinum*, *L. selago* and *L. clavatum* may be found on the lower slopes (down to

1200 ft.: 366 m.), but the two first-mentioned are more frequent on the summits (c. 1800 ft.: 549 m.). The presence, though in small quantities, of *Vaccinium vitis-idaea* and *Selaginella selaginoides* on the rocks near the summit introduces other arctic-alpine elements into the summit vegetation.

From some points of view the most interesting plant on Mynydd y Gader is *Genista pilosa*—a plant which is recorded only from one other locality (Pembrokeshire) in the Principality. The following quotation from a recent writer may be of interest. "*Genista pilosa*.—Hairy green weed. This rare plant was first recorded by Bingley in his Tour round North Wales (1800) from 'the foot of Cader Idris, between Dolgelley and Llyn Aran, about half a mile from the pool.' J. E. Bowman, a well-known botanist, is quoted in *The New Botanist's Guide to the localities of the rare plants of Britain*, by H. C. Watson, London (1835–7) as saying, 'I could not find it in the recorded situation, near Cader Idris.' Watson, in his *Topographical Botany* (1883), writes, 'An error.' The plant was rediscovered in fine quantities on the rocks near Mynydd Moel, Cader Idris, in June, 1901, by Mr James Backhouse, F.L.S., and the writer" (**12**). *Genista pilosa* occurs in a number of localities on the moorland between 1500 ft. and 1800 ft. (457 m. and 549 m.), and can be described as sparingly distributed. It was found by the present writer in 1927 in a peaty pocket on an outcrop of lower acid volcanic rocks at an elevation of nearly 1800 ft. (549 m.) and about a mile and a half from the "pool." This colony has been under observation since that time and a more detailed search has revealed the presence of ten such colonies in an area of about one square mile. Within this transect it grows in rock fissures on the outcrops of the lower acid volcanic rocks and of dolerite, with a southerly aspect, and generally beyond the reach of grazing animals. The plant assumes a prostrate habit, clinging closely to the surface of the rock, and except during the rather short and somewhat early flowering season it is very easily overlooked, even by the experienced field botanist.

On the small wet flats of the middle and lower slopes of the moorland where the water is stagnant and acid there are plant communities dominated by *Erica tetralix* often associated with an abundance of *Calluna vulgaris*. The composition of an *Erica tetralix* bog at about this level (1300–1500 ft.: 396–457 m.) is as follows:

Erica tetralix	d.	Juncus acutiflorus	o.
Juncus squarrosus	a.	J. communis	o.
Calluna vulgaris	f.—a.	Potentilla erecta	o.
Eriophorum angustifolium	f.	Festuca ovina	o.
Scirpus caespitosus	f.	Empetrum nigrum	o.—r.
Nardus stricta	o.	Sphagnum sp.	a.
Viola palustris	o.	Rhacomitrium lanuginosum	o.—f.
Agrostis alba	o.	Polytrichum commune	o.
Eriophorum vaginatum	o.	Cladonia sylvatica	o.

Again, along the courses of the small streams that drain the moorland, and in the flushes of the lower arctic-alpine zone there are communities that mark

the transition from acid peat to neutral soil. The Junceta of these (and lower) situations show two well-marked forms, viz. those dominated by *Juncus communis* and those by *Juncus acutiflorus*. In the zone of cultivation and rough enclosed pasture those dominated by the latter are the more extensive and common, but with increasing altitude they become less abundant and within this transect cease about 1750 ft. (534 m.). The *Juncus communis* consociation may be found up to 2300 ft. (701 m.). This high-level Juncetum (cf. **11**) is often characterised by an abundance of *Polytrichum commune* and by its relatively limited flora, as the following list will show:

Juncus communis	d.	Potentilla erecta	o.
Galium saxatile	a.	Viola palustris	o.
Oxalis acetosella	l.a.	Stellaria uliginosa	o.
Rumex acetosa	f.—a.	Eriophorum angustifolium	o.—r.
Agrostis alba	f.—o.	Eriophorum vaginatum	o.—r.
Aira caespitosa	f.—o.	Holcus lanatus	o.—r.
Cirsium palustre	o.	Juncus acutiflorus	r.
Deschampsia flexuosa	o.	Cardamine hirsuta	r.
Dryopteris dilatata	l.	Polytrichum commune	l.d.
Anthoxanthum odoratum	o.	(in bosses)	
Epilobium palustre	o.	Sphagnum sp.	l.a.

The Juncetum acutiflori is richer in species, of which the following is a representative list (1400–1600 ft.: 427–488 m.):

Juncus acutiflorus	d.	Ranunculus acris	o.
Galium saxatile	a.	R. flammula	o.
Potentilla erecta	a.	Oreopteris montana	o.
Ranunculus repens	a.	Athyrium filix-foemina	o.
Prunella vulgaris	a.—f.	Pinguicula vulgaris	o.
Cirsium palustre	f.	Triodia decumbens	o.
Hydrocotyle vulgaris	f.	Erica tetralix	o.
Scirpus caespitosus	f.	Festuca ovina	o.
Juncus squarrosus	f.	Blechnum spicant	o.
Viola palustris	o.—f.	Molinia caerulea	o.
Cardamine hirsuta	o.	Eriophorum vaginatum	l.
Epilobium palustre	o.	Phegopteris polypodioides	r.
Agrostis alba	o.	Empetrum nigrum	r.
Anagallis tenella	o.	Polygala vulgaris	r.
Aira caespitosa	o.	Calluna vulgaris	r.
Carex binervis	o.	Cardamine pratensis	r.
C. flava	o.	Cladonia sp.	o.
Juncus communis	o.	Hypnum sp.	a.
Anthoxanthum odoratum	o.	Sphagnum sp.	l.a.
Leontodon autumnalis	o.	Polytrichum commune	l.
Holcus lanatus	o.	(in bosses)	

C. *The zone of arctic-alpine vegetation* (Map 5).

On the summit plateau between Pen y Gader (2927 ft.: 892 m.) and Mynydd Moel (2804 ft.: 855 m.), on the precipitous sides of the corries or the steep face of the escarpment, and on the slopes between them and the moorland, there exists a type of vegetation which is distinct from that at lower levels: it represents plant life under the most extreme ecological conditions prevailing within the area and, in some respects, resembles that described for other high zones in the British Isles under the title of arctic-alpine vegetation.

Map 5. Zone of Arctic-alpine vegetation.

Legend (left column):

○ Moss-Lichen
Rhacomitrium Heath
Rm Rhacomitrium Moor

C Cryptogramme crispa
R-V Rhacomitrio-Vaccinietum
V-C Vaccinio-Callunetum
R Rhacomitrium (cushions)

-∙- High-level Grassland
-Cl- Gramino-Cladonietum
-V- Gramino-Vaccinietum
-R- Rhacomitrio-graminetum

⬦ Elevated Grass-moor
⬡ Elevated Wet-moor
Screes w Moraine
Cc Calluna vulgaris
Js Juncus squarrosus

Scale
0   ¼   ½   ¾   1 mile

Topographically, the most striking features of this high zone are the corries and the great rock ramparts: on the north or scarp slope is the main escarpment which reaches its greatest development between the Saddle and Mynydd Moel, that is, between the cwms or corries in which lie the tarns known as Llyn y Gader and Llyn Aran; on the south or dip slope is the magnificent cwm in which lies Llyn Cau bounded by another great rampart. These features end, rather abruptly, upwards in the monotonous rocky flat, the summit plateau; they pass, rather gradually, downwards into the moorland.

Geologically, the greater part of the summit plateau consists of the dip slope of the granophyre sill, the scarp edges of which form the greater part of the main escarpment (Pl. I, Phot. 1 and Map 2, section $X—Y$). This sill rests on a group of mudstones and ashes, at the base of which iron ore is often abundantly developed; the mudstones in their turn rest on the lower basic volcanic rocks which on their upper (stratigraphical) surface are frequently calciferous. Except where destroyed by the formation of corries or where covered with scree or moraine, this band of oolitic iron ore, and that of the calciferous "pillow lava" immediately underneath it, form a minor scarp which traverses the area from east to west under the main escarpment, forming a very distinct and, for survey purposes, a very convenient geological horizon. Near the summit of the mountain the granophyre sill is overlain by bands of mudstones and dolerite, followed at the actual summit by upper basic volcanic rocks; to the east of Mynydd Moel, where the granophyre comes to an abrupt end, the top of the escarpment is again capped by the upper basic group, the "pillow lavas" of which resemble those of the lower basic group in their calciferous nature.

In this zone of active denudation the amount of actual rock exposure is very great and the rock faces serve to emphasise the influence of the chemical nature of the substratum on the flora: the granophyre, dolerite and mudstones are comparatively sterile; but the basic volcanic rocks are often rich in plants.

An attempt may now be made to give a general account of the vegetation under four headings, viz. (1) the formation of mountain-top detritus, (2) the chomophytic vegetation of crags and corries, (3) the high-level (or "arctic-alpine") grassland, and (4) the vegetation of screes and moraines.

(1) *The formation of mountain-top detritus* (Pl. III, Phot. 5).

The summit plateau lies roughly between 2500 ft. (762 m.) and 2900 ft. (884 m.) and is thus a high altitudinal zone subject to the extremes of climate characteristic of all high mountain summits. The whole surface is fully exposed, at all times, to the force of the wind; it is subject to extremes of temperature; and it lies within a zone of high precipitation. Mists are prevalent at all seasons, and snow often covers the ground in winter; rain-bearing winds from the south-west are prevalent, but drying winds are rather frequent; and on clear days, in summer, there is intense insolation, while in winter frosts are common. Characteristic features of the higher parts are the stony wastes

which cover considerable areas: this rock débris which has accumulated *in situ* chiefly through the action of frost on the solid rock is known as mountain-top detritus. It is probable that the soil substratum over the whole surface consists of loose débris of this nature, but between the two extreme phases—the bare rock or stones and the "pockets" of peat in the small depressions—there are all possible gradations.

The plant covering as a whole consists of low growth forms which reflect the sum total of the climatic and edaphic factors just enumerated.

On the lower slopes of the summit plateau, on the small peaty flats at a higher level, and on the well-drained slopes with a thin covering of soil, there are modifications of subalpine moorlands already described or of "arctic-alpine" grassland to be considered later; but on the wind-swept northern edge of the plateau and for some distance down the dip slope in places where the ground consists of loose rock at, or very near, the surface are the two types of plant communities usually recognised as belonging to the formation of mountain-top detritus, viz. (*a*) the moss lichen open association, and (*b*) the *Rhacomitrium* heath closed association.

(*a*) *Moss lichen open association.* On stony ground and on very thin soil where the stony débris is still visible there exists a meagre vegetation consisting chiefly of mosses and lichens, but also of a few species of flowering plants which lead a precarious existence under severe climatic conditions. The rocky débris and the rock faces of the escarpment adjacent to this part of the plateau consist of granophyre—a rock which is nowhere rich in species. Thus, apart from climatic considerations, the paucity of the phanerogamic flora may be largely ascribed to the sterile nature of the substratum coupled with the poverty of the adjacent rock faces in plant species.

The flowering plants are characterised by a dwarf or prostrate habit and they generally occur as mats, cushions, or rosettes. *Empetrum nigrum* (o.) has a prostrate habit and clings very closely to the surface; *Vaccinium myrtillus* (f.) and *V. vitis-idaea* (o.) have dwarf shoots but long roots; and *Festuca ovina* (a.) occurs in the form of dwarf rosettes which are single plants with long fibrous roots (*c.* 4 in.: 10 cm.). Other flowering plants here are: *Galium saxatile* (f.), *Potentilla erecta* (a.) and *Campanula rotundifolia* (r.). The moss *Rhacomitrium lanuginosum* is, however, the most abundant and characteristic plant of these open situations. Associated with it, growing either on the small mats of this moss or on the "bare" soil (amongst others) are the following: *Lycopodium alpinum* (a.), (H.)[1] *L. selago* (o.—r.), *Polytrichum piliferum* (a.), *Cetraria glauca* forma (f.), (H.) *C. aculeata* forma *hispida* (a.), *C. islandica* (f.), *Sphaerophorus globosus* (o.), *Cladonia cervicornis* (f.) and *C. sub-cervicornis* (a.), and in greater or less abundance all the species of *Cladonia* mentioned later for the closed associations of the summit plateau. In addition to these *Lophozia floerkii, Scapania gracilis, Dicranella heteromalla* and var. *interrupta,* (H.) *Thamnolia*

---

[1] H. = "Highland" species in this and subsequent lists.

(*Cerania*) *vermicularis*, and *Baeomyces roseus* have been recorded for the moss-lichen open association of Cader Idris (**13** c). *Cetraria aculeata* f. *hispida* may occur as small round black balls clinging to the stems of *Vaccinium myrtillus*, but more commonly "parasitically" on the mats of *Rhacomitrium* where it forms black patches on the grey moss. On the "bare" rocks of the "islands" of débris the characteristic species are: *Rhizocarpon geographicum*, *R. oederi*, *Lecidea dicksonii*, *L. contigua* and forma *flavicunda*, *Rhacomitrium gracilescens*, *Andreaea petrophila*, and in particular the two lichens *Gyrophora cylindrica*[1] and (H.) *Parmelia pubescens*; between the boulders there are soft cushions of *Rhacomitrium lanuginosum* (with its "parasitic" lichens as above): towards the periphery of the "islands," as the boulders decrease in size and the decaying moss provides some measure of soil, such plants as *Vaccinium myrtillus*, *Festuca ovina*, and occasionally dwarf *Empetrum nigrum* become prominent; and on the extreme edge, where the débris is very fine and where there is a thin covering of soil, the open community passes into a closed association in which *Rhacomitrium lanuginosum* is generally dominant.

(*b*) *Rhacomitrium heath closed association.* It is impossible to draw a hard and fast line between the open communities and the *Rhacomitrium* heath: they pass into one another by a series of gradations. One of these transitional communities is that in which *Cladonia* spp. are co-dominant with the moss, forming a *Rhacomitrium-Cladonia* heath. *Cladonia furcata*, *C. gracilis*, *C. uncialis*, *C. sylvatica*, *Cetraria islandica* and *C. aculeata* f. *hispida* are the characteristic lichens of this community. Pure *Rhacomitrium* heath is difficult to find; but it occurs in detached patches near the summit of Mynydd Moel and along the edge of the escarpment, on thin black *Rhacomitrium* peat (2–3 in. or 5–7·5 cm. deep with a *p*H value of 5·6).

The following is a list of representative species:

Rhacomitrium lanuginosum	d.	Potentilla erecta	o.
Galium saxatile	a.	Vaccinium vitis-idaea	o.
(H.) Lycopodium alpinum	l.a.	(H.) Cetraria aculeata *forma*	o.
Cetraria islandica	l.a.	hispida	
Cladonia spp.	f.	Carex pilulifera	o.
Vaccinium myrtillus (dwarf)	o.—f.	Hypnum schreberi	o.
Polytrichum piliferum	o.—f.	Hylocomium loreum	o.
Festuca ovina	o.—f.	Campanula rotundifolia	o.—r.
(H.) Lycopodium selago	o.	Empetrum nigrum (dwarf)	o.—r.

Cladonia spp. include *C. sylvatica*, *C. furcata*, *C. rangiformis*, *C. gracilis* and *C. uncialis*.

In exposed flat parts of the summit plateau, on 6–8 in. (15–20 cm.) of black peat, a *Rhacomitrium* moor tends to develop. Such a community occurs

---

[1] The thallus of this lichen becomes crisp and hard in dry weather. This also applies to the Cladonias of the grassland on the summit plateau: the crispness and brittleness of the "carpet" in dry weather stands out in contrast to its softness in damp (not necessarily wet) weather.

on the elevated flat immediately to the east of Pen y Gader. The following is a list of characteristic species:

Rhacomitrium lanuginosum	d.	Sphagnum sp.	o.
Juncus squarrosus	s.d.	Deschampsia flexuosa	o.
Galium saxatile	a.	Cetraria islandica	o.
Polytrichum commune	f. (l.d.)	Plagiothecium sp.	o.
Vaccinium myrtillus (dwarf)	f.	Potentilla erecta	o.
Hylocomium loreum	a.—f.	Hypnum schreberi	o.
Luzula maxima	o.—f.	Agrostis sp.	o.
Festuca ovina	o.—f.	Eriophorum vaginatum	o.—r.
Nardus stricta	o.		

The formation of mountain-top detritus on Cader Idris is limited in extent and is not typically well developed. The vegetation is rather lower arctic-alpine in kind and in general takes the form of a grassland in which *Festuca ovina* is the dominant species.

(2) *Chomophytic vegetation.*

The great escarpment ranges in altitude from about 1800 ft. (549 m.) to over 2900 ft. (884 m.), but minor escarpments with a distinct representation of "Highland" species begin to be differentiated from the moorland at about 1500 ft. (457 m.): this gives a total vertical range of over 1400 ft. for arctic-alpine chomophytic vegetation on the northern slope of Cader Idris. After allowing for the normal and regular change of temperature with change of altitude it may be said that the weather conditions within this zone in general resemble those described for the summit plateau with certain qualifications. The scarp slope with its steep gradients is not subject to intense insolation as, at times, is the summit plateau, and during the winter months large portions of it do not receive sunlight at all and even in summer some parts receive little or no direct sunlight; the corries and the slopes of the great escarpment are protected from the full force of the prevailing wind and the atmosphere is generally more moist and humid than that about the summits. On the other hand edaphic conditions are different: the mountain-top detritus is porous and the rocks are acidic in character; on the escarpment moister conditions generally prevail and in parts the rocks have a relatively high calcium content. In addition, the variety of plant habitats on the scarps stands out in striking contrast to the monotony of the rocky flat.

The effect of increasing altitude on growth form and on distribution, the influence of the geological substratum on the variety and abundance of the vegetation, and the significance of the habitat in the determination of the nature of the plant communities, are aspects of the study of chomophytic vegetation that must be kept in view. For these purposes it will be convenient to consider the matter under three sub-headings, viz. (*a*) the "pillow lava" band of the lower basic volcanic rocks, (*b*) the upper basic volcanic rocks near Llyn Aran, and (*c*) the granophyre escarpment.

(*a*) *The "pillow lava" band (lower basic).* The lower basic volcanic rocks are not generally so resistant as other volcanic rocks within this area: it has

already been mentioned that the Upland Valley is a depression in these rocks. But towards their upper (stratigraphical) surface where lava predominates they are more resistant and, being also protected by the band of oolitic iron ore above them, they form the minor scarp already described. A characteristic feature of this lava is the development of "pillow" structure with small vesicles filled with calcite. This calciferous[1] lava has an important influence on the vegetation, as is shown by the abundance of plants compared with the adjacent areas and by the existence here of distinct calcicole species. These conditions prevail right across the transect (except where the calciferous rocks have been destroyed or covered as described), but they are best observed where the "band" reaches its greatest development, i.e. to the immediate south of Llyn y Gafr. Under Mynydd Moel the "band" is at its narrowest—only a few yards in width—but it is sufficiently well developed to show the contrast between the vegetation of the basic volcanic rocks and that of the adjacent intrusive masses of granophyre and dolerite: at the eastern extremity of the transect it widens again, but the vegetation, though often distinctly calcicole, does not compare either in variety or in abundance with that of the Llyn y Gafr rocks—floristically one of the richest localities in this part of the country.

The following is a list of distinctly calcicole species from this locality:

(H.) Saxifraga oppositifolia	l.a.	Arabis hirsuta	o.
(H.) Asplenium viride	f.	Adiantum capillus-veneris	v.r.
(H.) Cystopteris fragilis *forma*	f.	Hypnum commutatum	f.
dentata		Neckera crispa	f.—a.
Thalictrum minus	f.	Solorina saccata	f.
Pimpinella saxifraga	o.	Reboulia hemisphaerica	f.
(H.) Oxyria digyna[2]	r.		

It is noteworthy that *Asplenium viride* may be found all along the course of the "pillow lava" band within this transect, and that it rarely occurs off it: when the geological nature of the rocks is difficult to determine "in the field" the presence of this fern would almost certainly point to their calciferous nature and would be a rough guide to the course of the "pillow lavas." Though this band is a distinct geological horizon, it is not a geographical one: outside the area mapped it descends to much lower altitudes. *Asplenium viride* was not observed much below 1500 ft. (457 m.); but then the presence of such plants as *Reboulia hemisphaerica* and *Neckera crispa* unmistakably points to the calciferous nature of the rocks.

The following is a list of some other species from the same locality (altitude 1500–1700 ft. or 457–518 m.).

[1] Though the lavas constitute the most calcareous rocks in the Cader Idris sequence, a study of the flora shows that the ashes, also, both of the upper and of the lower basic volcanic series, are somewhat calcareous.

[2] *Oxyria digyna* is rare on the calciferous rocks of the lower basic volcanic series because of their relatively low altitude: on calciferous rocks of the upper basic volcanic series (in general above 1750 ft.: 534 m.) it is locally abundant.

(H.) Saxifraga hypnoides	l.a.
Chrysosplenium oppositifolium	l.a.
Luzula maxima	l.a.
Alchemilla alpestris	f.
Asplenium trichomanes	f.
Campanula rotundifolia	f.
Hymenophyllum peltatum	f.
Scabiosa succisa	f.
Thymus serpyllum	f.
Mecanopsis cambrica	o.—f.
(H.) Selaginella selaginoides	o.—f.
Veronica officinalis	o.—f.
Solidago cambrica	o.—f.
Adoxa moschatellina	o.
Anemone nemorosa	o.
Antennaria dioica	o.
Blechnum spicant	o.
Cardamine hirsuta	o.
Carex pulicaris	o.
C. flava	o.
Chrysanthemum leucanthemum	o.
Cryptogramme crispa	o.
Conium maculatum	o.
Dryopteris filix-mas	o.
Digitalis purpurea	o.
Deschampsia flexuosa	o.
Epilobium angustifolium	o.

(H.) Festuca ovina *forma* vivipara	o.
Geum rivale	o.
Geranium robertianum	o.
Hieracium sylvaticum (small forms)	o.
Hypericum pulchrum	o.
H. humifusum	o.
Linum catharticum	o.
Lathyrus montanus	o.
(H.) Lycopodium selago	o.
Oxalis acetosella	o.
Polygala vulgaris	o.
Pinguicula vulgaris	o.
Primula vulgaris	o.
Polypodium vulgare	o.
Phegopteris polypodioides	o.
P. dryopteris	o.
Ranunculus ficaria	o.
(H.) Saxifraga stellaris	o.
Sedum anglicum	o.
Solidago virgaurea	o.
Taraxacum vulgare	o.
Valeriana dioica	o.
Urtica dioica	o.
Viola sp.	o.
Asplenium ruta-muraria	o.—r.
(H.) Sedum roseum	r.

In addition the following lichens, mosses and liverworts may be mentioned: *Bartramia pomiformis* (f.), *Frullania tamarisci* (f.), *Fissidens adiantoides* (f.—a.), *Lecanora parella* (f. in large patches), *Lecanora tartarea* and probably *sub-tartarea* (a., in whitish patches, covering considerable parts of the rock surface), *Stictina fuliginosa* (l.a.), *Mnium undulatum* (f. in the shade), *Plagiobryum zierii* (f.), *Rhizocarpon petraeum* (f.), *Lecidea contigua* forma *calcarea* (o.—f.), *Aneura pinguis* (o.), *Pertusaria dealbata* (o.), *Polytrichum urnigerum* (o.), *Peltigera canina* (o.), *Scapania dentata* (o.), and *Sphaerophorus globosus* (o.).

Some of these plants, if not distinctly calcicole, show a preference for calciferous rocks: such are *Campanula rotundifolia, Selaginella selaginoides, Thymus serpyllum, Aneura pinguis* and *Antennaria dioica*. Others are distinctly calcifuge as, for instance, *Cryptogramme crispa, Digitalis purpurea, Blechnum spicant, Phegopteris polypodioides, Scapania dentata, Lecanora parella, Pertusaria dealbata* and *Sphaerophorus globosus*, as well as such plants as *Calluna vulgaris, Vaccinium myrtillus, Rhacomitrium lanuginosum* and others which are present though not included in the list. But most of the plants are "indifferent." The presence of acid humus on the rock ledges and of acidic rocks (intercalated with the calciferous lavas) may account for the presence of plants usually regarded as calcifuge (cf. **13** *a*).

As a result of the weathering away of the softer material intercalated with the lava, small caves or hollows are frequent at the base of the "pillow lava" band. Such situations, which form excellent shelter for sheep, are noteworthy for the presence of a "Lagerplatz" or "Lair" flora with nitrophilous species such as *Urtica dioica* and *Geranium robertianum*, the first named being particularly characteristic, occurring all along the course of the "band." In such

hollows "shade" plants such as *Anemone nemorosa* and *Adoxa moschatellina* (also nitrophilous) may be found locally. On the dry rock faces, in the small depressions in or around the "pillows" *Asplenium viride* is very dwarf (1–2 in.: 2·5–5 cm. long), but in damp places, particularly in the shade (as in the block scree under the Llyn y Gafr rocks), the fronds may be as long as 6 in. (15 cm.). On the rocks (*c.* 1500 in.: 457 m.) there are a few individuals of *Sorbus aucuparia, Fraxinus excelsior* and *Betula* sp.

(*b*) *The upper basic volcanic rocks* (near Llyn Aran). Like the "Gafr" rocks the cwm in which lies the tarn known as Llyn Aran ranks as a floristically rich locality. This is attributable to the presence of the basic "pillow lavas," which, however, in this case belong to the upper basic volcanic series. These rocks occupy the upper part of the escarpment which forms the southern wall of the cwm, and there is a striking contrast between the abundance and variety of the flora of these rocks and the barren nakedness of the wall of granophyre that forms its western flank.

The following list includes some of the plants from this locality (*c.* 1800–2400 ft.: 549–732 m.):

Adiantum capillus-veneris	v.r.	
Alchemilla alpestris	o.—f.	
Anemone nemorosa	o.	
Asplenium trichomanes	f.	
(H.) A. viride	l.	
Campanula rotundifolia	o.	
Carex binervis	o.	
C. flava	o.	
Chrysosplenium oppositifolium	l.a.	
Conium maculatum	o.	
Cryptogramme crispa	o.	
(H.) Cystopteris fragilis *forma* dentata	l.	
Dryopteris spp.	o.	
Epilobium angustifolium	o.	
E. palustre	o.	
Euphrasia officinalis	o.	
(H.) Festuca ovina *forma* vivipara	f.	
Filipendula ulmaria	o.	
Geum rivale	o.	
Hieracium sp.	o.—f.	
Hymenophyllum peltatum	o.	
Hypericum pulchrum	o.	
Lathyrus montanus	o.	
Luzula maxima	o.	
Lycopodium clavatum	o.	
(H.) L. selago	o.	
Molinia caerulea	o.—f.	
Oxalis acetosella	o.	
(H.) Oxyria digyna	l.a.	
Phegopteris polypodioides	f.	
Pimpinella saxifraga	l.	
Pinguicula vulgaris	o.	
Ranunculus repens	o.	
(H.) Rhinanthus crista-galli *forma*	r.	
(H.) Saxifraga hypnoides	l.a.	
(H.) S. stellaris	o.—f.	
Scabiosa succisa	o.	
Scirpus caespitosus	o.	
(H.) Sedum roseum	l.a.	
Solidago cambrica	o.	
S. virgaurea	o.	
Thalictrum minus	l.	
Thymus serpyllum	f.	
Veronica officinalis	o.	

Rhinanthus crista-galli forma was found in poor grassland, on a rocky ledge, at an elevation of about 2000 ft. (610 m.). All the plants seen (about ten in number) were unbranched and ranged from about 3 in. (with one flower) to about 6 in. (with three or four flowers). The flowering period extended from August to early September. The plant is not referable to any of the known mountain allies of *R. crista-galli*, but it may eventually be proved to be identical with an alpine form recorded from the Glyders by Dr Druce.

Cushions of *Anthelia julacea* and *Scapania dentata* are abundant on the rocks along the watercourses; *Lecidea contigua* forma *calcarea* occurs in whitish patches on rocks (not necessarily calciferous), and *Aneura pinguis*

and *Reboulia hemisphaerica* are frequent on the calciferous "pillow lavas." In the lower part of the escarpment the basic volcanic rocks are difficult to distinguish from the dolerites; but judging from the presence of distinct calcicole species (*Asplenium viride* and *Reboulia hemisphaerica*) it appears that the calciferous rocks descend, in parts, to the base of the escarpment. On the other hand, the presence of some of the calcicole species at the lower levels may be due to the influence of water trickling down from the pillow lavas of the upper levels[1]. Pockets of peat are frequent on the ledges and *Calluna vulgaris*, *Rhacomitrium lanuginosum* and other calcifuge species are frequent. *Calluna* is rather dwarf and it gives place with increasing altitude to *Vaccinium myrtillus*, generally in association with *Festuca ovina*. A few stunted individuals of *Sorbus aucuparia* (3–4 ft. high: 91–122 cm.) occur up to about 2000 ft. (610 m.). The upper basic volcanic rocks continue eastwards along (or near the top) of the ridge, outside the area mapped, and it is interesting to note that *Asplenium viride* may be found (though sparingly) along the calciferous band of these rocks; but owing to the absence of wet rock surfaces the vegetation here is nowhere abundant.

(c) *The granophyre escarpment.* On account of its altitude (c. 1800–2900 ft.: 549–884 m.) the great escarpment from Mynydd Moel to the Saddle is the habitat of a few notable plants which do not normally grow at lower levels; but on account of the absence of available lime the vegetation is distinguished neither by the variety nor even by the luxuriance of that on the basic volcanic rocks[2].

A large proportion of the surface is bare rock; but on the ledges dwarf *Calluna vulgaris* is frequent in the lower parts and *Vaccinium myrtillus* (also rather dwarf) in the upper parts. *Festuca ovina* and (H.) forma *vivipara* and *Rhacomitrium lanuginosum* are generally abundant; *Polytrichum commune* and *Sphagnum* sp. are locally abundant.

The following is a list of some characteristic species from the great escarpment (1800–2900 ft.: 549–884 m.):

Agrostis alba
Alchemilla alpestris
(H.) Armeria maritima *forma*
Athyrium filix-foemina
Blechnum spicant
Carex flava
Campanula rotundifolia
Cryptogramme crispa
Deschampsia flexuosa
Galium saxatile
(H.) Lycopodium selago
Luzula maxima
Molinia caerulea
Narthecium ossifragum
Oxalis acetosella
Phegopteris polypodioides

[1] In addition to the northern aspect of these rich localities, and to the presence of calciferous rocks, there is no doubt that the existence of *constantly wet surfaces* is an important factor determining the abundance of the vegetation.

[2] Percentage of CaO in granophyre, "eurite"; Llyn y Gader, Cader Idris = 1·94 (**Cole, G. A. J.** and **Jennings, A. V.**, *Q.J.G.S.* **45**, 1889). The percentage of CaO in the basic lavas of Cader not being available the following figures for similar rocks in the Dolgelley District may be given: "Spilite" (basic lava), Dduallt (Merioneth.) = 6·85 per cent., "Variolite" (from the outer part of a "pillow"), Craig-y-Benglog (Merioneth.) = 11·10 per cent. Analysed by **H. F. Harwood** (*Q.J.G.S.* **81**, pt 4, No. 324).

Pinguicula vulgaris
(H.) Plantago maritima *forma*   r.
Potentilla erecta
(H.) Saxifraga stellaris
Scabiosa succisa
Scirpus caespitosus
(H.) Sedum roseum   r.

(H.) Silene maritima *forma*   l.
Solidago cambrica
Sorbus aucuparia (about 4 ft. high,
    up to an altitude of 2300 ft.)
Thymus serpyllum
Viola riviniana

Cushions of (H.) *Anthelia julacea* and *Scapania* sp. are abundant on the wet surfaces in the gullies, and here also the moss *Tetraplodon mnioides* and the fungus *Peziza rutilans* may be found in association—saprophytic on the decayed bones of dead sheep. (H.) *Gyrophora cylindrica* and (H.) *Parmelia pubescens* which are frequent on the summit plateau may be found occasionally on the rocks at the base of the escarpment (c. 1800 ft.: 549 m.). *Andreaea petrophila, Lecidea dicksonii*, dark forms of *L. contigua*, and (probably) *Rhizocarpon confervoides* are abundant on the rock faces; but the large light patches of lichens (not necessarily calcicole) which are characteristic of the basic volcanic rocks are not present on the granophyre[1].

(3) *High-level (or "arctic-alpine") grassland.*

Within the arctic-alpine zone where the climatic conditions are not too severe, on all gently sloping ground with shallow and well-drained soil, there exists a type of grassland which is sufficiently distinct from grasslands at lower levels to merit separate treatment: though generally poor in "Highland" species, in some respects it resembles that described for similar habitats in other localities in the British Isles as "arctic-alpine" grassland. This grassland association may be found on parts of the summit plateau and even on well-

---

[1] Whilst no attempt has been made to give complete lists of plants on the crags in general it is believed that the plants named are fairly representative of the respective areas. The ground as a whole is difficult and much of it is quite inaccessible to the ordinary climber. Some interesting species have been recorded from the Cader Range, of which the most notable is (H.) *Salix reticulata*. In the *Journal of Botany*, vol. 50 (1912), C. E. Salmon writes as follows: "In the Power Collection in the Herbarium of the Holmesdale Natural History Club, Reigate, an example of *S. reticulata* exists labelled, 'N. Wales, Cader Idris.' Botanists visiting that fine mountain which rises to 2929 ft., would do well to try and confirm this record, as at present no other exists in Wales; the Cambrian localities mentioned by Ray for this plant really refer to *S. herbacea*." Again, in the *Cambridge British Flora*, vol. 2, the following note occurs: "We have seen the Merionethshire specimen above alluded to....The plant was gathered on Cader Idris at an altitude of about 890 m." As the culminating point of Cader Idris is only 2927 ft. or 892 m. the plant must have been found at or very near to the summit. It is almost certain that it is not present at (or about) this point to-day, but *if it does occur* on Cader the most likely locality is the calciferous portion of the basic volcanic rocks on the precipitous dip slope overlooking Cwm Cau, or at the top of the scarp slope to the north of the summit cairn. Amongst other species from the range are: (H.) *Salix herbacea* (not far from the summit), *Juniperus communis*, (H.) *Silene acaulis* (now said to be extinct), *Botrychium lunaria, Isoetes lacustris* (12); *Cochlearia alpina*, (H.) *Carex rigida* (2). From the summit (or very near) the following lichens and liverworts are recorded: *Ephebe (Ephebeia) hispidula, Pertusaria monogona, Coenogonium ebeneum, Stereocaulon denudatum* forma *pulvinatum, Lecidea albocoerulescens, L. crustulata, Psora confertula*, (H.) *Gymnomitrium concinnatum*, (H.) *Anthelia juratzkana*, (H.) *Lophozia alpestris, Marsupella stableri* and *M. emarginata* (at 2800 ft.: 854 m.) (13 c); and in a grassy patch on the Saddle between Pen y Gader and Mynydd Moel, there is an abundance of the moss (H.) *Webera commutata* (13 c).

drained ledges on the great escarpment, but it reaches its greatest development on the lower slopes where the high summits begin to be differentiated from the moorland. It is essentially a lower arctic-alpine community transitional in character between the subalpine and the upper arctic-alpine associations: on one hand it merges gradually into the moorland; on the other it passes through several gradations into the formation of mountain-top detritus. It may be subdivided as follows:

(1) A "dry" grassland on a porous substratum consisting of fine detritus (mountain top, scree, or moraine) with a very thin covering of dark soil and it may be a Gramino-Cladonietum, a Gramino-Vaccinietum, a Rhacomitrio-Graminetum or a more pure Festucetum ovinae.

(2) A grassland of mixed composition which usually occurs in the neighbourhood of springs and flushes ("flush grassland") or of rocks which provide shelter for sheep ("lair" grassland) in particular under the "pillow lava" band of the lower basic volcanic series. This grassland is remarkable for the presence of a relatively large number of "lowland" species.

(1) The following is a list of species with their relative frequency in the various forms of "dry" grassland.

(*a*) = Festucetum ovinae (*c*. 1600–1800 ft.: 488–549 m.).

(*b*) = Festucetum ovinae (*c*. 2000–2600 ft.: 610–792 m.).

(*c*) = Gramino-Vaccinietum (1800–2000 ft.: 549–610 m.).

(*d*) = Gramino-Cladonietum (summit plateau 2600–2900 ft.: 792–884 m.).

(*e*) = Rhacomitrio-Graminetum (*c*. 2700 ft.: 823 m.).

(*c*), (*d*) and (*e*) seem to be transitional communities between the "dry" grassland proper and the associations on mountain-top detritus or on screes.

	(*a*)	(*b*)	(*c*)	(*d*)	(*e*)
Agrostis sp.	o.	o.	o.	o.	o.
Anthoxanthum odoratum	o.	—	o.	—	—
Blechnum spicant	o.	—	o.	—	—
Campanula rotundifolia	o.	—	—	r.	r.
Carex pilulifera	—	o.—f.	o.—r.	o.	o.—f.
Cryptogramme crispa	—	—	l.	—	—
Deschampsia flexuosa	—	—	r.	—	—
Empetrum nigrum (dwarf)	—	o.—f.	f.—a.	o.—f.	—
Festuca ovina	d.	d.	c.d.	d.	c.d.
Galium saxatile	a.	a.	a.	a.	a.
Juncus squarrosus	o.	o.	o.	r.	o.
Luzula campestris	r.	—	—	o.	—
Lycopodium alpinum	a.—f.	f.—a.	f.—a.	f.	o.
L. clavatum	l.a.	o.—r.	o.—r.	r.	r.
L. selago	o.—f.	f.	o.—f.	f.	o.
Nardus stricta	o.—f.	o.	o.	r.	r.
Polygala vulgaris	o.	—	—	—	—
Potentilla erecta	o.—f.	o.—f.	f.	o.—f.	o.
Vaccinium myrtillus (dwarf)	f.	a.	c.d.	f.	f.—o.
V. vitis idaea	—	f.	a.—f.	o.—f.	—
Viola sp.	o.	—	—	—	—
Cladonia spp.	l.f.	l.a.	l.a.	s.d.	o.
Cerania vermicularis	—	—	—	l.	—
Cetraria aculeata *forma* hispida	—	—	—	o.	—
C. glauca	—	o.—r.	—	o.—f.	—
C. islandica	—	o.	—	o.	—
Rhacomitrium lanuginosum	f.	f.—a.	a.	f.	c.d.

Sphagnum sp., *Polytrichum commune*, *Hypnum* sp. and *Hylocomium* sp. may be abundant locally.

The following species of *Cladonia* are frequent on or near the summit of Cader Idris: *C. degenerans* forma *hypophylla* (on the rocks), *C. digitata*, *C. macilenta*, *C. floerkeana*, *C. rangiformis* and *C. sylvatica* (**13 c**). The dominant species in the grasslands seems to be *C. sylvatica*, but *C. rangiformis* may be abundant locally.

(2) On the lower slopes the ground is kept moist by the numerous springs that emerge here and there. Where the soil is peaty and the water acid such mosses as *Sphagnum* sp., *Polytrichum commune* and *Hypnum* sp. in association with *Juncus squarrosus* and *Nardus stricta*, are frequent; where the water is only moderately or slightly acid there are cushions of *Philonotis fontana*, *Brachythecium rivulare*, *Anthelia julacea* and *Scapania undulata* (higher levels) with associated plants of which *Saxifraga stellaris* (very dwarf, on the cushions of *Anthelia julacea* on the summit plateau) is the most characteristic; and under the band of calciferous "pillow lava" there are cushions of the moss *Hypnum commutatum* (Pl. IV, Phot. 6) with such plants as *Cirsium palustre*, *Cardamine hirsuta*, *Selaginella selaginoides*, *Saxifraga hypnoides*, *Chrysosplenium oppositifolium*, *Alchemilla alpestris* and very occasionally *Oxyria digyna*, in association. In addition, dark-coloured patches of the alga *Phormidium autumnale* may be found here and there near these springs, and in the water inside the "trial level" for iron ore under Mynydd Moel, the liverwort *Cephalozia bicuspidata* is abundant.

In the neighbourhood of these springs and flushes on the lower arctic-alpine slopes of the northern flanks of Cader Idris (*c.* 1500–1800 ft.: 457–549 m.) under the band of calciferous rocks there occur small detached grassland communities of mixed composition (but dominated locally by *Festuca ovina*, *Agrostis vulgaris* or *Poa annua*) notable for the presence of lowland plants, some of which occur as arctic-alpine varieties or forms. Amongst these are the following: *Achillea millefolium* (f.), *Bellis perennis*[1] (l.a.), *Campanula rotundifolia* (l.), *Cerastium vulgatum* (o.), *Cirsium palustre* (l.a.) (red and white flowers), *Dactylis glomerata* (o., dwarf), *Euphrasia officinalis* (l.a.), *Plantago lanceolata* (f.), *P. major* (o.), *Polygala vulgaris* (o.), *Prunella vulgaris* (f.), *Leontodon autumnalis* (l.), *Oxalis acetosella* (o.—f.), *Ranunculus acris* (o.), *R. repens* (o.), *R. ficaria* (o.), *Rumex acetosa* (o.—f.), *R. acetosella* (o.—f.), *Stellaria media* (o.), *Triodia decumbens* (o.), *Viola* sp. (o.), *Trifolium repens* (l.a.), *Veronica officinalis* (o.), *Thymus serpyllum* (o.) and *Sagina procumbens* (o.).

Strictly speaking, these grassy patches cannot be described as calcareous grasslands owing to the absence of the species that usually characterise such communities, although the distinctly calcicole species *Saxifraga oppositifolia* may be present locally; but the high quality of the herbage[2]—in this respect

---

[1] *Bellis perennis* is said to be entirely absent from the open sheep walks of mid-Wales (**2**).

[2] On the other hand, the "dry" grassland (*a*) and (*b*), which is, in no sense, a calcareous grassland, provides very good pasturage for sheep; even parts of the summit plateau rank high, in this respect.

rivalling the best parts of the zone of cultivation—and the presence of the lowland species must be largely ascribed to the influence of the calciferous rocks of the lower basic volcanic series.

(4) *Screes and moraines.*

Two other topographical features of some geological and botanical interest within this zone of active denudation are the small crescentic moraines at the open ends of the small cwms or at the foot of the main escarpment, and the screes under the precipitous rock faces. The moraines are evidence of local glaciation which took place towards the close of the glacial period and belong to a relatively mature physiography where soil development is rather far advanced: the screes bear witness to the action of frost and water on the rocks during post-Glacial times and range from relatively mature features such as undisturbed old screes to the unstable half-cones of rocky débris in course of formation at the present time.

As plant habitats the screes and, to some extent, the moraines at this level resemble mountain-top detritus: physiographically, they consist of loose rocky material ranging from large blocks to fine débris; edaphically, they show all stages of soil development from bare rock to a covering of soil; and climatically, they are subject to extremes. They differ from mountain-top detritus, however, in the greater depth of their débris and in the greater porosity of their soils, in their more sheltered situation resulting from the level at which they occur, and, in the case of "shingle slips," in the mobile state of the débris.

The vegetation thus resembles that of the formation of mountain-top detritus in the structure of the plant communities, but differs from it in its floristic composition and growth form.

For the sake of convenience of description but also from edaphic considerations the vegetation of screes[1] (and to some extent of moraines) may be grouped as follows:

(*a*) Open communities consisting chiefly of individual plants which are scattered on ground composed of loose rocky débris (cf. (**14**) "individual habitat").

(*b*) Semi-closed communities consisting of groups of plants which themselves may be closed communities but which are separated by bare rocky débris ("colony habitat").

(*c*) Closed communities that completely cover the ground composed of fine débris with a thin covering of soil.

(*a*) A considerable portion of the talus slope at the foot of the great escarpment is composed of loose rocky débris almost entirely devoid of vegetation: mobility or instability renders the débris unsuitable as a plant

---

[1] Roughly these may be designated open scree, patchy scree, and covered scree, respectively.

Phot. 7. "Twr Du" (2676 ft.: 816 m.) from the moorland, looking south. The grass moor (Nardetum strictae) in the foreground passes into "high-level" grassland, and then into a wilderness of stone (moraine and half-cone screes). The ploughed screes (on right) are the result of a great storm (summer, 1926). The small black patches between the ploughed screes are ericaceous colonies which have developed on a peaty substratum on the scree.

Phot. 6. *Hypnum commutatum* cushion in spring at the base of the "pillow-lava" band (Lower Basic Volcanic Group). *Cirsium palustre* on the periphery of the cushion: calcareous scree on the slope above.

EVANS—CADER IDRIS: A STUDY OF CERTAIN PLANT COMMUNITIES IN SOUTH-WEST MERIONETHSHIRE

habitat. But as the blocks become more settled and the gaps between them are filled with finer material they become the habitat of certain plants which are adapted for life under such conditions. Notable amongst these on the arctic-alpine slopes of Cader Idris is the Parsley Fern (*Cryptogramme crispa*)—a plant which is local in its distribution in the British Isles in general but which grows in profusion in this particular locality and is the scree plant *par excellence* (cf. **15**). In similar situations the following plants may be found: *Phegopteris dryopteris*, *P. polypodioides*, *Blechnum spicant*[1], *Galium saxatile*, *Saxifraga stellaris* (one of the first invaders), *Festuca ovina* and forma *vivipara*, *Deschampsia flexuosa*, *Digitalis purpurea* (f. in one locality, 1600–1800 ft. or 488–549 m.; height of some of the plants in flower, 2 ft. 6 in. or 76 cm.), *Cirsium palustre* (local), *Lycopodium selago*, *Oxalis acetosella*, mosses such as *Rhacomitrium lanuginosum*, *Polytrichum urnigerum* and *P. commune*, as well as individual plants of *Vaccinium myrtillus*, and seedlings of *Calluna vulgaris*. On the rock débris the moss *Grimmia doniana* is of frequent occurrence.

Under the escarpments containing calciferous rocks such plants as *Asplenium viride*, *Cystopteris fragilis* var. *dentata* and even *Oxyria digyna*[2] may occur as scree plants. It thus seems that the screes are largely recruited, with respect to species, from the adjacent rock faces.

(*b*) Though *Cryptogramme* may be the most notable plant on the talus slope the most abundant plant and the most important soil former is the moss *Rhacomitrium lanuginosum*. At the foot of the talus slope or at the base of the inner slope of the moraine, where the rock débris consists of large blocks, and over wide areas in a wilderness of rocks, it may be the only plant present apart from the small patches of mosses and lichens on the blocks. Occasionally the cushions of this moss, which fill the spaces between the rocks, are invaded by lichens such as *Cladonia* spp. and *Cetraria islandica* and even by ericaceous plants. *Rhacomitrium lanuginosum*, by its growth and decay, forms the foundation for the ericaceous colonies that are characteristic of the lower parts of the talus slopes (Pl. IV, Phot. 7). The first stage in the development of these colonies seems to be the invasion of the cushions or mats of *Rhacomitrium* by *Vaccinium myrtillus* and communities which may be described as Rhacomitrio-Vaccinieta cover extensive areas of the upper talus slopes. With further decay of the moss and the accumulation of relatively deep peat (up to 1 ft.: 30 cm.) these communities are invaded by *Calluna vulgaris* and pass, on the lower talus slopes, into the second and final stage at these altitudes—the Vaccinio-Callunetum (or occasionally into purer Calluneta).

---

[1] One form of the fern *Blechnum spicant*, with the fronds dichotomously branched at the apex, was found at 2000 ft. (610 m.): on Mynydd y Gader (at 1500 ft.: 457 m.) another form was found with very short or contracted pinnae on the lower half of the frond.

[2] In one case this plant trailed underground for a distance of about 1 ft. (30 cm.) before emerging through the scree.

The following are the characteristic species of the two communities:

Rhacomitrio-Vaccinietum		Vaccinio-Callunetum	
Rhacomitrium lanuginosum	c.d.	Calluna vulgaris	d.
Vaccinium myrtillus	c.d.	Vaccinium myrtillus	s.
Galium saxatile	a.	Vaccinium vitis-idaea	f.
Empetrum nigrum	l.a.	Festuca ovina	o.
Festuca ovina and *f.* vivipara	o.—f.	Lycopodium selago	o.
Lycopodium alpinum	o.—f.	Blechnum spicant	o.
Cryptogramme crispa	o.	Deschampsia flexuosa	r.
Lycopodium selago	o.	Lycopodium clavatum	r.
Potentilla erecta	o.	Cryptogramme crispa	r.
Agrostis sp.	o.	Rhacomitrium lanuginosum	o.—f.
Deschampsia flexuosa	o.	Hypnum schreberi	l.a.
Carex pilulifera	o.	Plagiothecium sp.	o.
Calluna vulgaris	o.	Scapania sp.	l.
Blechnum spicant	o.	Sphagnum sp.	l.a.
Anthoxanthum odoratum	o.		
Luzula maxima	o.		
Lycopodium clavatum	o.—r.		
Hylocomium loreum	l.a.		
Polytrichum commune	f.		
Cladonia sp.	o.		

(*c*) On parts of the talus slope and on the tops of the moraines where the substratum consists of fine detritus in a stable condition a form of grassland tends to develop. According to the relative frequency of *Vaccinium myrtillus*, *Cladonia* spp., and *Festuca ovina* this grassland community may be a Gramino-Vaccinietum, a Gramino-Cladonietum or a more pure Festucetum ovinae. These have been described already under the heading "High-level" (or "arctic-alpine") grassland.

4. DISCUSSION.

Here and there in the course of the description of the vegetation an attempt has been made to analyse some of the phenomena or at least to state some of the problems to be solved: it is now proposed to consider some of these problems in greater detail and in particular to indicate the lines along which investigation is proceeding.

The history of the vegetation since the close of the Glacial Epoch must be interpreted in the light of information as to the sequence of events gained from the study of the submerged forests and the more recent lowland peats of the coastal and estuarine flats, the upland or moorland peats, the zonation of the present vegetation, and the relict flora.

Up to the present no detailed examination of the submerged forests and the peats of the foreshore has been undertaken according to modern methods of peat investigation, but mention may be made of certain features the study of which may eventually throw some light on the succession of the vegetation on the coastal fringe. "At Barmouth, it is on record that the rock bottom of the Mawddach was traced by the cylinder foundations of the railway viaduct to 40 ft. below the level of low water, where it was shelving rapidly downwards beneath a bed of peat of unascertained thickness, but too deep to be penetrated

for foundations[1]." In several localities round the coast, submerged forests are exposed at low water, the trees of which near Barmouth "appear to have been mainly birches[2]," while at Borth to the south of the Dovey estuary, "many, perhaps the great majority, of the larger tree stools on the foreshore undoubtedly belong to *Pinus sylvestris*" (6); the forest was succeeded by a "moorland phase, which may have commenced or extended owing to the subsidence of the land. Moorland conditions still obtain over a considerable portion of the Dovey Flats, but the area of moorland has been circumscribed by the encroachment of the sea" (6).

Pine probably reached the British Isles in pre-Boreal Time soon after the immigration of the *willows* and the *birches*, and the pinewoods reached their maximum post-Glacial development with the oncoming of milder climate in Boreal Time. Towards the close of the Boreal and especially during the warm, moist, Atlantic Period the pine disappeared as an element in the forests or remained only as a relict in odd places. In Scotland, however, in the Grampians, large pine forests have persisted to the present day. With the oncoming of warm, dry, continental, conditions during the sub-Boreal Period the pine reached a secondary maximum, especially in the northern parts of Great Britain and Ireland, but during the succeeding cold moist sub-Atlantic Period degeneration again set in (16, 17 b).

It has been suggested that the pine trees growing on the Borth Flats at the present day may be relics of the old pine (submerged) forest off the coast (6). Pollen statistical study of the moorland peat on the Flats would go far towards determining this point. On the other hand, assuming that the submerged (upper) forest belongs to the late "Neolithic" Period, then the forest itself must be a relict or be derived spontaneously from relict pinewood in the district.

To the north of the area, in Scotland (in the estuary of the Clyde for instance) the equivalents of these submerged forests are to be found in the raised beaches; in the Isle of Man there is evidence of a slight sinking; but on the Lancashire coast (as at Heysham) there is some evidence of more marked subsidence, probably to the extent of about 60 ft. (18 m.); to the south of the area, "it seems that the Bristol Channel points to a subsidence in post-Glacial times of about 60 ft." and "that in Cornwall...old land surfaces can be found far below (about 70 ft.) the sea-level" (8). At Leasowe, off the coast of Cheshire, there are two forest beds and the upper bed exhibits a close floristic resemblance to, and may thus be fairly contemporaneous with, the base of the Pennine peat and with the base of the mosses on the 25-ft. beach of Wigtownshire, which were formed during the Atlantic Period (9 a and ref.); "at the base of the superficial forest bed off Rhyl in North Wales a polished stone axe has come to light" (20); on the coast of Pembrokeshire there are at

---

[1] Codrington, T. G. B., *Q.J.G.S.* 54, 251 and reference.

[2] Osborn, T. G., "A note on the submerged forest at Llanaber, Barmouth," *Manchester Lit. and Phil. Soc.* 56, No. 16, 1912.

least two distinct layers of forest; and at Barry, in Glamorgan, the excavation for the extension of the docks showed four distinct levels of peat, in the lowest of which were "much broken oakwood, mixed with seeds, and freshwater shells...hazel, cornel, hawthorn, burreed, and sallow" and in the highest were "logs of willow, fir and oak" and a "Neolithic worked flint" (8).

Taking all these statements into consideration, it seems that, during the submerged forest period, not only was there a distinct contrast between the conditions prevailing in the north and those in the south of Britain, there was also much variation locally in the submerged areas themselves, and perhaps in the time when the forests of the coastal fringe disappeared.

The buried wood (mostly twigs) at the base of the peat on the divide across the Upland Valley consists mostly of *Salix* and *Betula*, the species of which are difficult to determine owing to the poor state of preservation. During Arctic[1] or sub-Arctic Time it is probable that the ground round the melt-water which collected in the hollows and slacks on the top of the moorlands (1700–1800 ft.: 518–549 m.) was invaded by high arctics and high alpines and by such temperate plants as had survived the rigours of the last glaciation. In the course of time, owing to growth of the vegetation and silting-up of the channels, the ground was prepared for invasion by trees such as the *willow* and the *birch*— probably the first immigrants into the area. Pending further work on these deposits it may be permissible to assume that the base of the Cader peats belongs to the pre-Atlantic Period (if it is not actually pre-Boreal in point of time). There is some evidence that the degeneration of the woodland or scrubland took place as the result of a change of climate from relatively dry to moist conditions and the onset of this degeneration may be placed, provisionally, at the end of the Boreal Period or early in Atlantic Time[1].

[1]

Glacial Time	——— to 10,200 B.C.	
Arctic Time	10,200 B.C. to 8,800 B.C.	
Sub-Arctic Time	8,800 B.C. to 7,500 B.C.	
Boreal Time	7,500 B.C. to 5,500 B.C.	Climatic Periods
Atlantic Time	5,500 B.C. to 2,500 B.C.	
Sub-Boreal Time	2,500 B.C. to 500 B.C.	
Sub-Atlantic Time	500 B.C. to ———	
Palaeolithic Time	——— to 6,500 B.C.	
Epi-Palaeolithic Time	6,500 B.C. to 4,500 B.C.	
Neolithic Time	4,500 B.C. to 2,000 B.C.	Archaeological Periods
Bronze Age	2,000 B.C. to 500 B.C.	
Iron Age and Historical Time	500 B.C. to ———	

The climatic periods are the Blytt-Sernander Climatic Periods of Scandinavian geologists and botanists, and the chronology is, more or less, based on the geo-chronology of Gerard de Geer. (For more detailed information concerning these climatic and archaeological periods see ERDTMAN (16) and WOODHEAD (17 *a* and 17 *b*).) Speaking generally, the time scale is applicable to the whole of north-western Europe; but adjustments may be necessary in dealing with particular areas. For instance, in Wales, with part of which this paper deals, "Bronze Age" culture may have survived until the eve of the Roman conquest (20).

' In the Baltic region, during late Glacial, Arctic and early sub-Arctic Times much of the land

Undoubtedly, peat is forming in parts of the moorland at the present time, but a slight degeneration is also taking place as the result of the cutting back of the heads of the streamlets into some of the plateau flats. Peat has also been removed through human agency from parts of the summit of Mynydd y Gader, though not perhaps within living memory. It seems probable that some, at least, of the mixed bogs represent stages in the infilling of moor pools and that a kind of rhythmic process has been going on—an alternate up-building through the growth of the vegetation and a down-breaking through the actions of the small streams, helped by the upward growth of the bog. The presence of islands of undenuded peat in the moor pool—remnants of the old bog, the peat-filled former outlets of the pools—and the re-invasion of the wet denuded area by *Eriophorum angustifolium* denoting the first stage in the formation of the new bog (regeneration), seem to support this view. Retrogression is also taking place on parts of the summit plateau, notably on Mynydd Moel, as the rather frequent "lakes of stones" seem to indicate; and it has been suggested (**13** *b*) that the abundance of *Cladonia* spp. in the *Rhacomitrium* heath denotes retrogression. The "islands" of detritus (mountain-top) show a progression from bare rock to a thin covering of soil: on the contrary the "lakes of stones" may show a retrogression from soil covered by some form of plant community to bare stones. At the same time it must be noted that extensive degeneration such as is occurring at the present time on the moorlands of the southern Pennines and also, as Prof. O. T. Jones tells me, in the Plynlimmon area, though probably to a less extent than on the Pennines, is not in evidence in this area.

The natural form of vegetation in the lowland zone is woodland, and where it has escaped destruction[1] it extends up the slope to about 1100 ft. (335 m.): at about this level it changes through scrubland to moorland. The buried wood in the peat shows that at least some parts of the moorland were "forested" at one time up to an elevation of slightly over 1750 ft. (533 m.) and postulates a depression of the tree line by about 650 ft. (199 m.). The transition from woodland through scrubland to moorland reflects the change in existing

surface was occupied by an ice-dammed lake and in late sub-Arctic Time, with the final withdrawal of the ice, the *Yoldia Sea* was formed: in Boreal Time the cutting off of the Atlantic resulted in the formation of the *Ancylus Lake*; and in Atlantic and early sub-Boreal Time when connection with the Atlantic was re-established, the area was occupied by the *Littorina Sea*.

In Britain, some time during the Glacial Period the ice sheet blocked the northern outlet of the North Sea and the water found its way out over the col where now lies the Strait of Dover (**8**); some time after this, when the climate had ameliorated—in pre-Atlantic Time—elevation of the land converted a large part of the North Sea into an alluvial plain and turned the Strait of Dover into a "land bridge"; but in late Boreal and chiefly in Atlantic Time subsidence set in—the alluvial plain was submerged and the present Strait of Dover was formed.

[1] Three localities (in the Mawddach, Dulas and Dovey Valleys respectively), however, come within the scope of the Government Afforestation Scheme. The trees already planted are, mainly, Scots and Corsican Pine, European and Japanese Larches, Douglas Fir, Norway and Sitka Spruces (Annual reports of the Forestry Commissioners).

"local" climate—chiefly in the increase of rainfall with increased altitude and the consequent accumulation of peat: the change from woodland or scrubland to moorland, as revealed in some of the peat hags situated well above the present limit of trees, suggests a radical change of climate—a change from relatively dry to wet conditions—as the primary cause of the depression of the tree line. Peat began to accumulate around the bases of the trunks of the trees—a process that finally led to the degeneration of the forest.

In the zone of cultivation and rough enclosed pasture, the woodlands, destroyed directly or indirectly as a result of human activity, have given place, largely, to rough enclosed pastures or "ffridds." The study of the vegetation of the "ffridd" resolves itself into the study of the gradual conquest of the old ground flora of the former woodland by pioneer species of more open situations, and again, as a result of direct human interference, of the gradual displacement of this natural vegetation consisting of plants of low nutritive value by herbage of better quality. The future of the "ffridd" as pasture lies in the extension of the better parts (*G, H*, in the tables, p. 17) at the expense of the *Nardus-Molinia* grassland, in the suppression of *Pteridium* and *Ulex*, in the draining of the bogs and swamps, and in the subdivision of the "ffridd" into sections by the erection of wire fences in order to provide for the better regulation of the cropping[1].

As to the relict flora Cader Idris has a fair representation of "Highland" species, comparing favourably in that respect with the less elevated Plynlimmon (2468 ft.: 752 m.) to the south, where *Saxifraga stellaris* and *Salix herbacea* are the only recorded representatives (2), but unfavourably with the more elevated mountains in the Snowdon district to the north where such plants as *Juncus triglumis, J. biglumis, Saxifraga nivalis, Dryas octopetala, Saussurea alpina, Draba incana, Arabis petraea, Cerastium alpinum, Thalictrum alpinum*, in addition to most of those on Cader Idris, are the representative species.

Again it is interesting to note that certain "Highland" species which are more or less common in the north of England and Scotland are entirely absent from North Wales as a whole. "As examples the following may be cited: *Primula farinosa, Cherleria sedoides, Saxifraga aizoides, Alchemilla alpina.* These, with others not met with here (in Snowdonia) are common in the mountains of northern England as well as in those of Scotland. They undoubtedly formed constituents of the main flora which had been driven southward during the last Glacial Epoch, and on the return of warmer conditions had again spread in a northward direction. Why did they fail to effect an entrance into North Wales? Doubtless the absence of calcareous rock on the western routes may help in part to account for the difficulties in the way of Welsh immigration that some of them failed to surmount. But this would not explain the absence of *Alchemilla alpina*, a common inhabitant of the northern hills, unless indeed it had already passed northwards before the ice barrier

---

[1] See the report on the College Farm (1927), The Dept. of Agric., U.C.N.W. Bangor.

which closed the western passage was unlocked. Perhaps in the stress of competition to occupy the few available spots, those species failed to secure a sufficient lodgment whence they might spread at leisure. The bulk of the species, having travelled northward, had left behind too few individuals to spread as successful colonists in the face of their more numerous competitors" (**18**). On the other hand the Snowdon district is the only known locality for *Lloydia serotina* in Britain. "It is a difficult problem to account for its existence in this region, for though it occurs in arctic lands and extends into North America, its main centre lies along the great chain that extends through the Alps of Europe to the Himalayas of Asia. If it be a relic of the northward plant migration at the close of the Glacial Epoch it is difficult to account for its absence from the Cumbrian and Scotch mountains" (**18**).

The elevated parts of Cader Idris are excellent ground for the study of the formation of screes and of the successional development of vegetation. The talus slope of the great escarpment is composed of a series of half-cone screes with their apices at the lower ends of the numerous gullies cut into the vertical rock faces. In maturity of feature the screes as a whole range from young scree where the disintegration of the adjacent rock face is greatest, to old scree where it is least; and each individual half-cone scree ranges from the unstable "shingle slip" at the apex to the relatively mature formation at the base. "Shingle-slip" vegetation, that is, vegetation on "active" scree or scree proper is an open plant community consisting almost entirely of individual plants. There is here little or no succession, that is, no reaction of species on species: the substratum is generally *porous* and *unstable* and successional development is impossible. As the scree becomes more stable, the substratum still remaining *porous*, there may be successional development, either true succession or physiographic succession, from open plant communities through various grades of transitional stages to the high-level grassland —the climatic climax at these elevations. On the other hand, where the ground becomes more stable and the substratum *loses its porosity* peat may accumulate and there may be true succession from open communities to closed "ericaceous" colonies—the edaphic climax. These colonies, however, are not essentially different to other subalpine moorland communities at this high elevation, that is, they may be regarded as particularly elevated subalpine moorland communities developed under peculiar edaphic conditions and not as typical scree communities.

5. SUMMARY.

1. Proximity to the western sea-board (*c.* 52·5° N., 4° W.), a varied topography, a high range of altitude, the presence of rocks of diverse chemical and physical natures, coupled with the activities of the inhabitants, are the master factors governing the vegetation of the Cader Idris area.

2. The area falls readily into three altitudinal zones of vegetation: (*a*) the zone of cultivation and enclosed hill-pasture; (*b*) the moorland zone; (*c*) the zone of arctic-alpine vegetation.

3. Within the transect the zone of cultivation and enclosed hill pasture consists of arable land, meadows and associated pastures, and of plantations and remnants of former woodlands: the moorland zone comprises patches of heather moor, of wet moor and a considerable area of grass moor; and the zone of arctic-alpine vegetation includes the formation of mountain-top detritus, chomophytic vegetation of crags and corries, the vegetation of screes and of moraines, and a high-level grassland which in some respects resembles arctic-alpine grassland.

4. Mixed deciduous woodlands of the valley bottoms in which the oak— generally *Quercus robur* (*pedunculata*)—is the dominant species pass in places, especially with increasing altitude, into sessile oakwoods (Querceta sessiliflorae): these in their turn, with still increasing altitude, pass into birchwoods (Betuleta). The hybrid oak, *Q. robur* × *sessiliflora*, is rather frequent in the oakwoods and the hybrid birch, *Betula alba* (*verrucosa*) × *pubescens*, dominates the birchwoods. The arable land, meadows and associated pastures are generally on stony loam of glacial or of alluvial origin; but some of the meadows are on peaty land which bears the distinctive name of "rhos." The enclosed hill pasture or "ffridd" is on the site of former woodland and is generally— especially the Upper Ffridd—a *Nardus-Molinia* grassland with facies in which *Pteridium aquilinum*, *Ulex gallii*, *Agrostis vulgaris* and *Festuca ovina* assume local dominance.

5. The scarp slope of Cader Idris is too rocky to allow for the development of typical heather moor, but patches of heather (*Calluna vulgaris*) cover parts of the lower slopes of the moorland. On the moorland plateau flats small mixed bogs are numerous, and wet-moor communities are arranged in more or less concentric zones around moor pools: these bogs may be described in general as Sphagno-Eriophoreta from the dominant species. The rest of the moorland consists chiefly of grass moor in which *Nardus stricta* is generally fully dominant. But along the courses of the streams and in the flushes, Junceta occur, and these are of two distinct forms: (*a*) those dominated by *Juncus communis*; (*b*) those dominated by *J. acutiflorus*. The *J. acutiflorus* communities cease at about 1800 ft. (549 m.) and the high-level Junceta are dominated by *J. communis*. Buried wood, consisting mainly of *Betula* sp. and *Salix* sp., occurs near the base of the peat on some of the moorland flats at an elevation of about 1750–1800 ft. (533–549 m.).

6. The formation of mountain-top detritus includes the moss lichen open association, the *Rhacomitrium* heath closed association, and a transitional community between them known as *Rhacomitrium-Cladonia* heath. The vegetation of the talus slopes resembles that of the formation of mountain-top detritus: it consists of open plant communities which, on favourable soils, pass

through transitional communities into high-level grassland—the climatic climax at these elevations, or on unfavourable soils (i.e. peaty soils) into Vaccinio-Calluneta (or more pure Calluneta) which may be regarded as examples of elevated moorland associations within the arctic-alpine zone. The chomophytic vegetation of crags and corries consists of some "Highland" species, of alpine forms of maritime plants, and of some distinct calcicole species. The floristically rich localities coincide with the outcrop of the "pillow lavas" of the lower and the upper basic volcanic series. The arctic-alpine vegetation of Cader Idris belongs chiefly to lower arctic-alpine associations and a high-level grassland covers most of the slopes and of the summit plateau. This grassland may be subdivided into (*a*) a "dry" grassland which is generally a Festucetum ovinae with transitional communities which may be described as Gramino-Vaccinieta, Gramino-Cladonieta or Rhacomitrio-Gramineta, and (*b*) a grassland of mixed composition which is noteworthy for the presence of a relatively large number of lowland species. This grassland (*b*) is not, strictly speaking, a calcareous grassland, but the presence of lowland species and the high nutritive value of the herbage may probably be attributed to the influence of the calciferous rocks.

6. ACKNOWLEDGMENTS.

REFERENCES.

(1)   **Carr, H. R. C.** and **Lister, G. A.** *The Mountains of Snowdonia.* John Lane, The Bodley Head, London, 1925.

(2)   **Salter, J. H.** "The altitudinal range of flowering plants and ferns in mid-Wales." *North-Western Naturalist,* **3,** Nos. 3 and 4, 1928.

(3)   **Cox, A. H.** "The geology of the Cader Idris Range (Merioneth.)." *Quart. Journ. Geol. Soc.* **81,** Pt. 4, No. 324, London, 1925.

(4 a)   **Cox, A. H.** and **Wells, A. K.** "The lower Palaeozoic rocks of the Arthog-Dolgelley district (Merionethshire)." *Quart. Journ. Geol. Soc.* **76,** Pt. 3, No. 303, London, 1921.

(4 b)   **Cox, A. H.** and **Wells, A. K.** "The geology of the Dolgelley district, Merionethshire." *The Geologists' Assoc.* London, 1927.

(5)   **Lake, P.** "Bala Lake and the river system of North Wales." *Geol. Mag.* **7,** New Series, Decade 4, London, 1900.

(6)   **Yapp, R. H., Johns, D.** and **Jones, O. T.** "The salt marshes of the Dovey estuary." This JOURNAL, **4,** 1916.

(7 a)   **Jones, O. T.** "The origin of the Manchester plain." *Journ. Manchester Geol. Soc.* **39–40,** 1923–24.

(7 b)   **Jones, O. T.** "The origin of the Welsh legends." *The Welsh Outlook,* Newtown, Mont., 1921.

(8)   **Reid, Clement.** *Submerged Forests.* Cambridge, Univ. Press, 1913.

(9 a)   **Evans, E. Price.** "Warburton moss (Cheshire)." This JOURNAL, **16,** No. 2, 1928.

(9 b)   **Evans, E. Price.** "Carrington moss (Cheshire)." This JOURNAL, **11,** No. 1, 1923.

(10)   **Williams, J. Lloyd** and **Robinson, G. W.** "Reclamation of peat-lands in Carnarvonshire." *Brit. Assoc. Rep.* 1917.

(11)   **Pethybridge, G. H.** and **Praeger, R. Ll.** "The vegetation of the district lying south of Dublin." *Proc. Roy. Irish Acad.* **25,** Sect. B, No. 6, Dublin, 1905.

(12)   **Jones, D. A.** "The flora of Dolgelley and the neighbourhood." Append. 3 in *The Story of Two Parishes* (see footnote, p. 10).

(13 a) **Watson, W.** "The bryophytes and lichens of calcareous soil." This JOURNAL, **6,** 1918.

(13 b) **Watson, W.** "The bryophytes and lichens of arctic-alpine vegetation." This JOURNAL, **13,** No. 1, 1925.

(13 c) **Watson, W.** "Field notes on the flora of Cader Idris." (Not published.)

(14)   **Allan, H. H.** "Notes on the study of the open communities of high-mountain areas in New Zealand." Chap. 22 in *Aims and Methods in the Study of Vegetation* (Brit. Emp. Veg. Committee).

(15)   **Leach, W.** "A preliminary account of the vegetation of some non-calcareous British screes (Gerölle)." This JOURNAL, **18,** No. 2, Aug. 1930.

(16)   **Erdtman, G.** "Some aspects of the post-Glacial history of British forests." This JOURNAL, **17,** No. 1, Feb. 1929.

(17 a) **Woodhead, T. W.** "History of the vegetation of the southern Pennines." This JOURNAL, **17,** No 1, 1929.

(17 b) **Woodhead, T. W.** "The forests of Europe and their development in post-Glacial Times." *Empire Forestry Journal,* **7,** No. 2, 1928.

(18)   **Farmer, J. B.** "Notes on the flora of Snowdonia." Chap. 8 in *The Mountains of Snowdonia.* John Lane, The Bodley Head, London, 1925.

(19)   **Burkill, I. H.** and **Willis, J. C.** "Botanical notes from north Cardiganshire." *Journ. of Botany,* Jan. 1894.

(20)   **Wheeler, R. E. M.** *Prehistoric and Roman Wales.* Oxford, Clarendon Press, 1925.

Phot. 1. The Bakuriani Basin. The Imeretin Hills are to the right and Tzhra-Tzharo to the left.

SEIFRIZ—SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA. III. PLANT LIFE IN THE BAKURIANI BASIN, MINOR CAUCASUS

SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA

III. PLANT LIFE IN THE BAKURIANI BASIN, MINOR CAUCASUS

By WILLIAM SEIFRIZ.

(With Plates V–VIII, and four Figures in the Text.)

THE Minor Caucasus Mountains, often referred to as the Trans-Caucasus, lie south of the main Caucasus range in the Soviet Republic of Georgia (Gruzia). At their base, seventy miles west of Tiflis, is the town of Borjom. Near by, though a mile higher, resting among the most lofty peaks of the Minor Caucasus, is the little mountain village of Bakuriani; it lies a trifle south of the 42° parallel.

Few places are more picturesque than the basin formed by the hills surrounding Bakuriani (Pl. V, Phot. 1). The little valley is a garden of great charm, quite different from the wild and harsh snow-capped High Caucasus to the north, the dry hills of Turkey and Armenia to the south, the parched semi-desert steppes of Tiflis to the east, and the humid shores of the Black Sea to the west. Bakuriani gives one the quiet and beauty of an English pasture, with the not too rugged character of unglaciated mountains. The hills forming the base are most inviting to the botanist. The flora is rich and varied, and the plants so distributed as to present interesting ecological problems.

It is the purpose of this article to describe the plant life growing in late summer in the Bakuriani Basin. Brief reference will be made to a few characteristic plants found at a lower level, and to two uncommon species occurring just over the basin rim: otherwise, we shall remain strictly within the basin.

The present article is the third in a series of five on plant life in the southern countries of the Soviet Union. In each of these articles I have allowed the final identification of the specimens collected to rest with taxonomical specialists who either reside within the respective regions or are recognised authorities on the flora there. The final identification of the plants mentioned in the present article was made by Mr L. V. Koslovski, Director of the Botanic Station at Bakuriani, and Mr M. S. Timofeev of Tiflis; to each of these gentlemen I am indebted for this and many other courtesies extended to me during my sojourn at Bakuriani. My thanks are also due to Mrs N. A. Maximov for arranging trips in a most efficient and helpful way, and to Mrs M. S. Timofeev for kindly sketching the *Campanula* in Fig. 4.

The climate of Bakuriani is mild in summer and not unduly severe in winter. The average July–August temperature is 15° C., and the January–
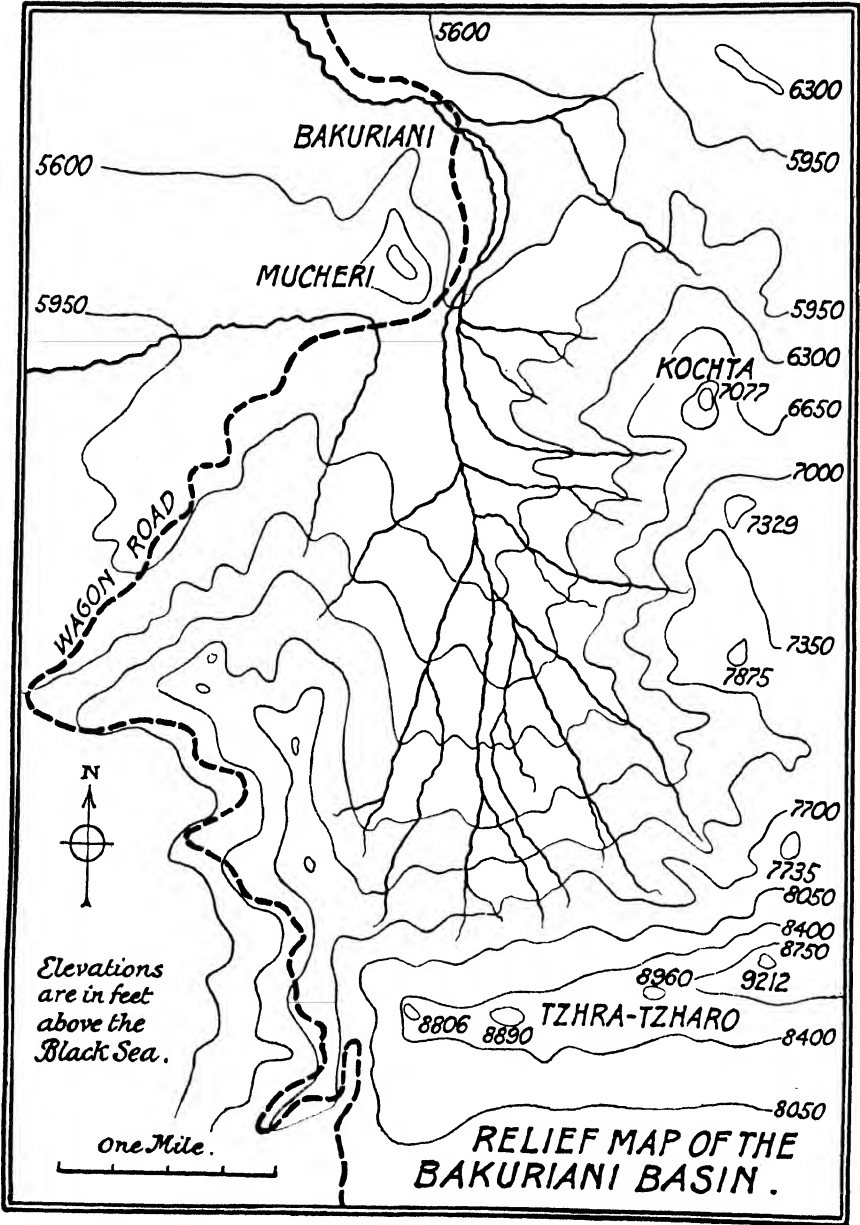
Fig. 1.

February temperature − 9° C. None of the nearby mountains have perpetual snow upon their summits. The peaks and plateaux which form the basin, rise to a maximum height of 9212 ft., which is 3600 ft. above the basin floor, the altitude of Bakuriani being 5600 ft.[1] (Fig. 1). If we view the panorama from the village, facing south, and name the hills from east to west (left to right) we have (Fig. 3): first, Kochta; then, the three Kochta Hills which lead to the high plateau of Tzhra-Tzharo, where the maximum altitude of the basin rim is reached; next, the Imeretin Hills leading down to a small valley which forms one of the outlets of the basin; then, across the valley where, immediately on our right, lies the knoll Mucheri. We are now back at the village of Bakuriani with valleys leading to the right and left. The basin is completed by the Shugliat Ubani Mountain Range running east and west and lying to the north, that is, at our back as we view the panorama from the village. We shall study, in turn, the flora of each of these mountains as just enumerated.

The zones or belts—Schimper prefers the term "regions"—of plant life on a mountain side are distinguished by certain characteristics of a rather definite nature wherever the country; thus, there is usually a lower dense forest, then a higher open forest of smaller growth, next, subalpine fields, and finally, alpine pastures. Zacharov[2], in his study of the high mountain soils of the Caucasus, divides these mountains into the following three main belts, with eleven minor divisions: I, Forest belt, (1) mixed coniferous-deciduous, (2) beech, (3) pine, (4) forest meadows: II, subalpine belt, (5) scattered birch with high grass, (6) dry meadows with scattered pine, (7) high grass meadows: III, alpine belt, (8) rhododendron, (9) alpine meadows of medium grass, (10) alpine carpet of low grass, (11) mountain steppe meadows.

Zacharov's classification of all the Caucasus would do fairly well for the Bakuriani Mountains, but it fails to call attention to some of the outstanding features of plant life on these hills, and, on the other hand, refers to distinctions which are not to be found here. Since our purpose is to understand and appreciate the flora of the Bakuriani Basin rather than to fit our observations into any general tabulation, we can simply divide the mountain slopes into those five zones which we meet and easily distinguish, one after another, as we climb. These five zones readily fall into the belts given by Zacharov.

---

[1] My inconsistency in the use of metres (in the first two articles of this series) and of feet (in the present article) is due to the indiscriminate use of metres, feet, and sashen in Russia. It was at first my intention to change all units to metres, but where, as in the case of Bakuriani, all information as to altitudes and distances, was received in feet, and contour maps scaled in sashen, which are readily transposed into feet by multiplying by seven and thus yielding round numbers, I not only found it more convenient for myself but believe it will be less confusing to the reader to retain the foot as the unit in the present article.

[2] **Zacharov, S.** *On the characteristics of the high mountain soils of the Caucasus* (in Russian). Moscow, 1914.

No.	Altitude (ft.)	Zone	Type genera
0	5600–5800	Bakuriani fields	Pirus, Gramineae
I	5800–6500	Lower mixed forest	Fagus, Picea, Pinus
II	6500–6700	Upper forest; deciduous on the north, coniferous on the south	Acer, Pinus
III	6700–7000	Open subalpine woods	Betula, Sorbus, Pinus
IV	7000–8000	Subalpine meadows	Herbaceous plants
V	8000–9000	Alpine fields and rocky precipices	Antennaria, Rhododendron

The Bakuriani Fields, 5600–5800 ft.

The village of Bakuriani is surrounded by the usual pastures and cultivated fields of any small mountain village. Enough trees occur, especially at the base of the hills, to give to the valley floor a distinctive type of arboreal vegetation. The altitude of Bakuriani (5600 ft.) marks the upper limit of a number of species which grow in great profusion lower down, and also the lower limit of many mountain forms. The scattered trees of the village pastures thus serve as a connecting link between the high and the low mountain forests.

Pines and spruces are abundant both above and below Bakuriani. The spruce, *Picea orientalis*, is the outstanding tree of the Minor Caucasus. The pine, *Pinus hamata* (Pl. VI, Phot. 2), is about as numerous and forms fine specimens, but the spruce at its best is unsurpassed in size and number. The distribution of these two conifers is of interest in that the pine shows no preference for altitude, occurring from the sea coast to the highest rocky subalpine regions, while the spruce has a very definite altitudinal distribution, being at its best at 5000–6000 ft. and not occurring much above 6500 ft.: on the other hand, the pine prefers southern exposures, while the spruce shows little or no preference for the points of the compass.

Apart from the pines and spruces, an abundant and characteristic tree on the Bakuriani Basin floor is the wild pear, *Pirus communis*. The apple, *P. malus*, also occurs. Wild pears, apples, cherries, and plums occur throughout the mountains of the Russian Provinces along the 42° parallel. We have seen *Pirus elaeagnifolia* in the Crimean Mountains[1] and we shall meet *Pirus malus* again in great numbers in the lower mountain gorges of eastern Turkestan[2]. Below Bakuriani, at 5000 ft. grows the wild plum, *Prunus divaricata*.

Ulmus elliptica, *Corylus avellana*, and *Acer platanoides* find their upper limit at Bakuriani. *Corylus* is a "tree shrub" rarely attaining more than 15 ft. in height. *Quercus macranthera* is at home here though it is not very abundant. *Alnus glutinosa* and a single specimen of *Fraxinus excelsior* occur.

Two specimens of *Abies nordmanniana* grow in the woods near Bakuriani, but the species is typical of a lower altitude (4500 ft.) where it occurs with the spruce.

---

[1] "The altitudinal distribution of plants on the Crimean Mountains."—See this JOURNAL, XIX, No. 2, pp. 361–371.

[2] "Plant Life of the Transilian Mountain Range in Semirechje, Eastern Turkestan."—See this No., pp. 78–88.

Phot. 3. *Betula pubescens* (*B. caucasica*) near the summit of Kochta.

Phot. 2. *Pinus hamata.*

SEIFRIZ—SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA. III. PLANT LIFE IN THE BAKURIANI BASIN, MINOR CAUCASUS

Sky Line of Kochta and adjoining Mountain Ranges, showing Distribution of Trees, as seen from the West.

MEADOW?
PINUS
ACER
BETULA
QUERCUS
FAGUS
PICEA
KOCHTA

FAGUS

PICEA, PINUS
PICEA, FAGUS.
SHUGLIAT UBANI

ROCK
PINUS, PICEA
GVIRGVINA

Fig. 2.

An enumeration of some of the outstanding plants occurring just below Bakuriani will give an idea of the marked change in species type which takes place here at the base of the upper mountain peaks. *Acer platanoides*, only an occasional inhabitant of the Bakuriani Basin floor, is abundant in the mixed forest below 4500 ft. where it forms superb large specimens. Two other maples grow at this lower altitude, *Acer campestre* and *Acer lactum*. *Quercus iberica*, one of the most numerous of the oaks, *Tilia vulgaris*, a good grower, and *Carpinus betulus*, rare at Bakuriani, are all frequent inhabitants of the lower forests.

Of the three species of *Sorbus* occurring in the Caucasus, *aucuparia, torminalis*, and *aria*, all are to be found near Bakuriani. *S. aucuparia* is very abundant at higher altitudes (7000 ft.). *S. aria* grows near the village on the south slope of the Shugliat Ubani (5700 ft.). *S. torminalis*, whose leaves, like those of *aria*, are simple as compared with the pinnate ones of *aucuparia*, is found only below Bakuriani (4500 ft.).

Crataegus monogyna is rare at Bakuriani and numerous below. *Rhamnus cathartica, Viburnum orientale, Lonicera caprifolium, L. orientalis, Hedera colchica, Campanula crispa*, endemic for Armenia, *Sedum maximum, Philadelphus caucasicus (P. coronarius)*, and *Ostrya carpinifolia*, are all characteristic of the mountain slopes just below Bakuriani and are not to be found above.

The survey of plant life described in this article was made in late August, 1929. Few meadow flowers are to be seen at Bakuriani at this time of year, yet one is now at its best, *Colchicum speciosum*; this and its smaller sister, *C. umbrosum*, form luxuriant patches on wet ground.

Carices are numerous; *C. pairaei* is an inhabitant of the lower meadows, also *C. vesicaria* and *C. gracilis* (var. *angustifolia* and *tricostata*); *C. silvatica* grows on the borders of the forests; *C. caespitosa* occurs a little higher up (on Kochta); and *C. hirta* is in the Bakuriani marshes.

KOCHTA.

Zone I. The first of the hills that we shall climb is Kochta (Fig. 3), which, while not among the highest of the mountains, offers a most varied and interesting flora. It lacks one thing in that it is not high enough to harbour truly alpine vegetation.

The Georgian who named Kochta the "Elegant" was well aware of the stateliness of the mountain. The summit is 1400 ft. above Bakuriani with a total altitude of 7077 ft. We shall climb the mountain on the west slope.

At the base of Kochta there is a mixed coniferous-deciduous forest, with *Picea orientalis* predominating. *Fagus orientalis* forms the chief deciduous tree, and is fairly abundant. *Quercus macranthera* is occasionally present.

The spruces are unusually fine at the base of Kochta, some developing into superb trees with a maximum height of 125 ft. and a diameter of 4 ft. They are at their best on the west slope.
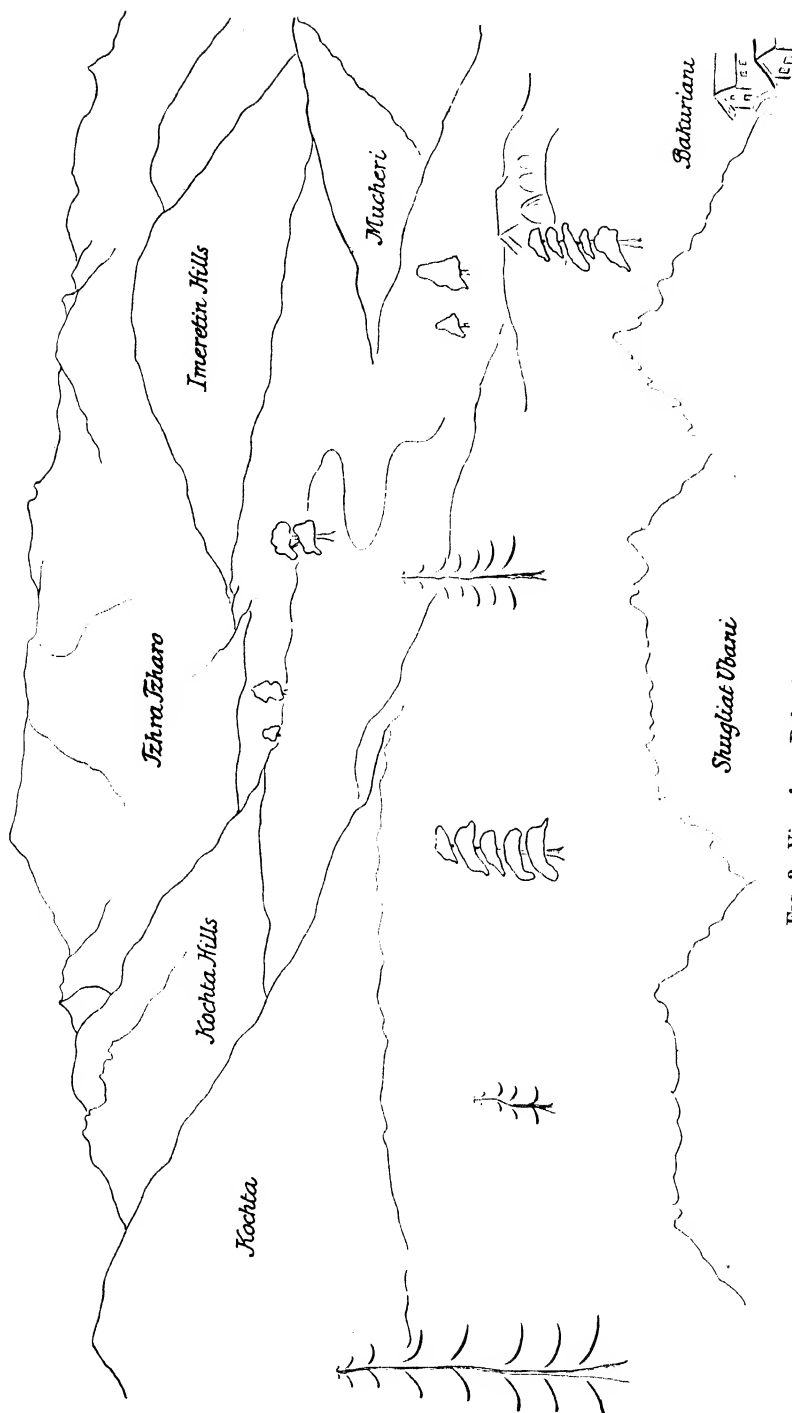
Fig. 3. View from Bakuriani, looking south.

If one wanders far enough to the right and left of Kochta one can observe the pronounced north and south distribution of pine and beech, which is more clearly marked on Mucheri just across the valley. The north slope of Kochta is chiefly beech. The south slope is almost solely pine. Spruce predominates on the west slope up which we are walking. On the south, the pine continues to the top or just short of it, while on the north, the beech soon gives way to birch.

Woody shrubs occurring in the mixed spruce-beech forest at the base of Kochta are: *Ribes biebersteini*, *R. alpinum*, *Viburnum lantana*, and *Rubus idaeus*.

The lower forest of Kochta is well developed, but it encloses small open meadows where flourishes a rich herbaceous flora, among which the following may still be found in flower during late August: *Digitalis ferruginea* with its conspicuous spike, the yellow-flowered *Lapsana grandiflora*, the tall-growing weed *Valeriana alliariaefolia*, the large leaved (70 cm.) *Petasites officinalis* (*albus*) growing in wet ravines, the gentian, *Gentiana asclepiadea*, the arrow-leaved *Mulgedium cacaliaefolium* with small blue composite flowers, *Sedum oppositifolium* on rocky slopes, and the three grasses *Festuca gigantea*, *Poa longifolia*, and *P. nemoralis*. *Ophioglossum vulgatum* occurs sparingly.

Mosses are not abundant. The following three well-known North American species (kindly identified by Mr R. S. Williams of the New York Botanical Garden) were collected: *Dicranum bonjeani*, *Ptilium crista-castrensis*, and *Pleurozium schreberi*. Five species of *Usnea* festoon the trees in moderate quantity. In addition to the two species collected and given in the following list, there also occur *Usnea florida* var. *sorediella*, *U. longissima*, and *U. barbata*. No attempt was made to observe an altitudinal distribution of the lichens at Bakuriani though I do not doubt that such a distribution occurs, as it does to a striking degree in Java[1]. Here I shall put all the lichens collected into one list, stating only that they come from within the Bakuriani Basin. The identification of the lichens has been done by Prof. Charles C. Plitt of Baltimore, to whom I am grateful for this courtesy.

1. Buellia parasema	16. Parmelia sulcate
2. Cladonia pyxidate neglecta	17. Parmelia tubulosa
3. Evernia esorediosa	18. Peltigera canina
4. Gyrophora spodochroa	19. Peltigera horizontalis
5. Lecanora chlarona	20. Pertusaria leioplaca
6. Lecanora pallida	21. Pertusaria scutellata
7. Lecanora rubina	22. Physcia grisea
8. Lecanora subfusca	23. Physcia pulverulenta
9. Lecanora sp.	24. Physcia pulverulenta angustata
10. Lecidea (Biatora) sp.	25. Physcia stellaris
11. Leptogium saturninum	26. Ramalina populina
12. Letharia divaricata	27. Rinodena sophodes
13. Ochrolechia pallescens	28. Usnea hirta (U. florida var. hirta)
14. Parmelia glabra	29. Usnea scabrata
15. Parmelia saxatilis	

[1] "The Altitudinal Distribution of Plants on Mt Gedeh, Java." *Bull. Torrey Bot. Club*, **50**, 283, 1923. See also this JOURNAL, **12**, 307–313, and Plate VII, 1924.

Phot. 5. Pine right (south), beech left (north), on the knoll Mucheri: *Corylus avellana* and *Populus tremula* as undergrowth in foreground.

Phot. 4. Pine right (south), birch left (north), near the summit of Kochta.

SEIFRIZ—SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA. III. PLANT LIFE IN THE BAKURIANI BASIN, MINOR CAUCASUS
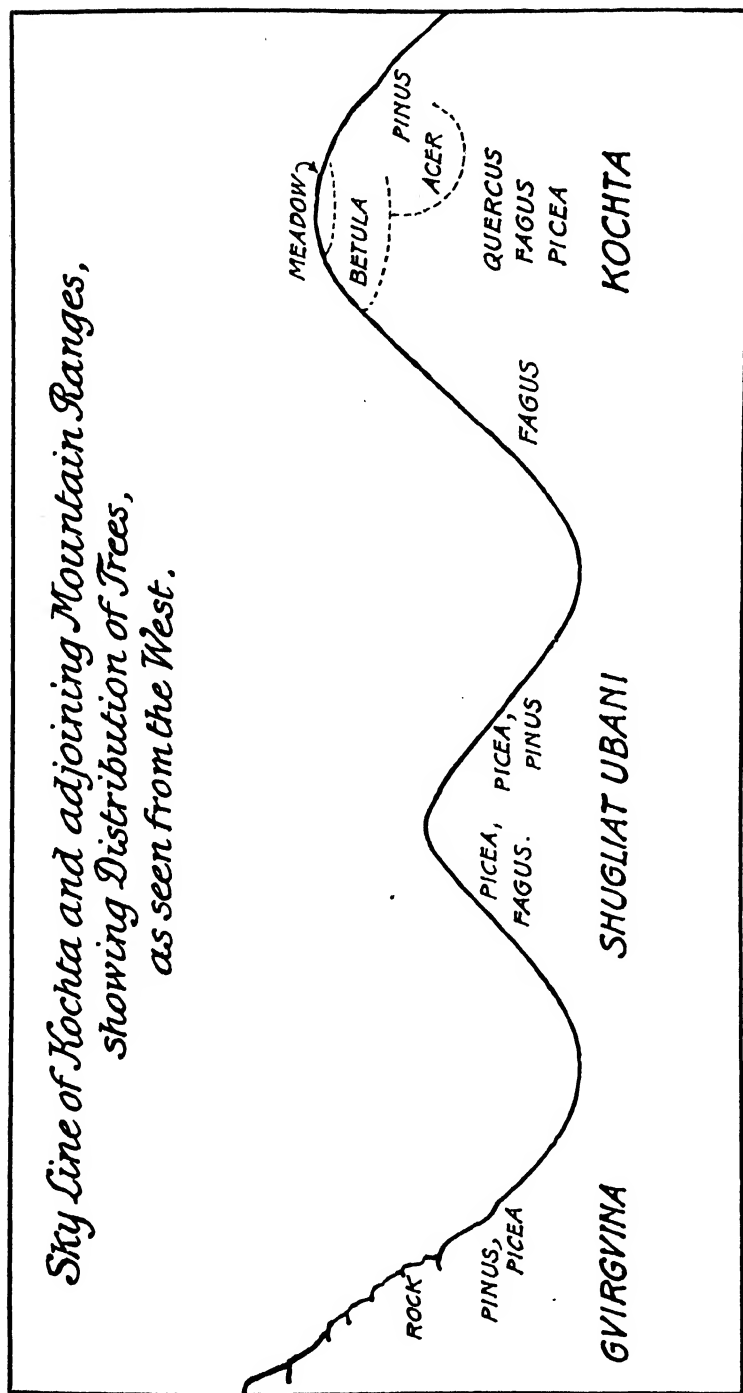
Nos. 3, 24 and 29 seem to be restricted to that part of the world in which they were collected. Nos. 4, 17, 19, 21 and 22 are European. The remainder are cosmopolitan.

Zone II. At 6500 ft. the last of the spruces is passed on the climb up Kochta. The upper limit of *Picea orientalis* is sharply marked. There are no scattered specimens creeping up to higher ground here and there. The beech continues a little above the spruce, so also does Bakuriani's only oak, *Quercus macranthera*. The outstanding tree at this altitude (6600 ft.) is the maple, which predominates to such a degree that at a distance its light green foliage masks all else.

The upper deciduous forest on Kochta, from 6500 to 6700 ft., is a mixed association of maple, with a few scattered oaks, the last beeches, the first birches, and *Sorbus*. The maple is *Acer trautvetteri*, the only species of this genus occurring above Bakuriani. It is endemic to the Caucasus. *Acer trautvetteri* was brought by Radde in 1864 from an altitude of over 1800 metres in the higher Caucasus and was identified by Trautvetter as *A. platanoides*. Later Medwedew recognised the plant as a new species which he named *trautvetteri*. Radde[1] states that this maple reaches the tree line in many places in the Caucasus.

Open meadows, within the forest, become more and more numerous as one climbs. They enclose an interesting group of plants which in small areas may consist of but a single species in profuse flower. The tall and attractive *Campanula lactiflora* is abundant in the woods at this altitude (6500 ft.); so also *Gentiana septemfida* and the tallest of the gentians *G. asclepiadea*. A little higher, where the maples are at their best, *Heracleum wilhelmsii* is to be found.

Zone III. Once out of the maple forest at 6700 ft., one meets an open association of *Betula pubescens* on the left (north) and *Pinus hamata* on the right (south). The line of division of birch to the north and pine to the south, is so sharp that the trail on the crest of the west ridge, along which we are walking, separates birch from pine without either getting on the other side of the trail (Pl. VII, Phot. 4). The birch forms the tree line on the north slope of Kochta, shares this honour with the pine on the west slope, and yields entirely to the pine on the south.

The birch growing here is generally recognised as *Betula pubescens*, though it has received the name of *B. caucasica* with *B. pendula* as a synonym. *B. verrucosa* is also in these mountains but at a lower altitude. The birches are a difficult genus. Cuttings from the same tree are often identified differently. The birches on Kochta are the finest of any of the mountain specimens of this typically Russian tree that I saw in the southern Soviet Union (Pl. VI, Phot. 3): they compare favourably with the birches of the lowlands, of the open country from Samara to Moscow; no tree is more beautiful, especially when seen in its autumnal foliage.

---

[1] **Radde, G.** *Pflanzenverbreitung in den Kaukasusländern* (*Die Vegetation der Erde*, III), Leipzig, 1899.

Looking down to the right one sees that the entire southern slope of Kochta is covered with the pine, *Pinus hamata*. The identification of the Bakuriani pine I left to my associates Mr Koslovski and Mr Timofeev; they regard the pine as *P. hamata*. Radde does not mention *P. hamata*, using *P. silvestris* throughout for this species. He also gives *P. montana* for the Caucasus, but cautions against confusing it with the low scrubby form of *P. silvestris* which is abundant, while *P. montana* is not. Formin gives both *P. silvestris* and *P. hamata* for the Bakuriani region, believing the former to grow on the north slopes and the latter on the south. (Since pine on northern slopes is rare then *P. silvestris* would not be often met with.) Sosnovsky states, "I am of the opinion that on all slopes there occurs only one species, namely, *P. hamata*, which is not only the pine of the Trans-Caucasus but probably of all the Caucasus."

The habitat of *P. hamata* is as varied as its distribution is wide; it occurs on the edges of alpine pastures in company with *Rhododendron*, and in Sphagnum bogs and salt marshes on the shores of the sea. Another species of the Trans-Caucasus (its identity is not in doubt) is *P. armena* which is limited to the extreme south (Turkey).

The tree line on the north side of Kochta, at 7000 ft., is of *Betula* mixed with *Sorbus aucuparia*; on the south, it is pine, and the pines go to the very base of the mountain while the birches extend down but a short distance, where they are replaced by maples.

Subalpine pastures are scattered in the birchwoods and pinewoods. They increase in area until they unite to form the treeless meadow which is the summit of Kochta. The open character of these birchwoods and pinewoods permits a rich herbaceous undergrowth, the individuals of which are chiefly the subalpine plants of the summit of Kochta, with some of the gentians and campanulas already met with.

Zone IV. The summit of Kochta (7077 ft.) is a rounded cap covered with a thick carpet of grasses and subalpine herbaceous plants. Alpine pastures are often regarded as essentially grass, but this is not true here, nor in the high Caucasus. In the latter region subalpine meadows may support a rich herbaceous growth practically devoid of grass[1]. The proportion of herbaceous specimens to grasses in the higher alpine meadows above Bakuriani, has been estimated by Timofeev to be 30–40 species of herbaceous plants as compared with 8 species of Gramineae (*Poa* predominating), while in subalpine regions, such as the summit of Kochta, the number of herbaceous species may be 70–80 to 8 of grasses. Although the difference between herbs and grasses is great in number of species, the bulk of the two at haying time may be nearly equal.

The small pasture which crowns Kochta harbours an abundance of

flowering plants of which many are still in flower during late August, though the blossom may be the last of the season. The ever-present and superb *Scabiosa caucasica* is found with the yellow-flowered *Cephalaria tatarica*. These two plants characterise subalpine fields throughout the Caucasus. The delicate blue flower of *Podanthum campanuloides* is sparingly intermixed with the fine large purple flowers of *Betonica grandiflora*; this latter plant covers the fields in spring. There are four gentians above Bakuriani, *G. septemfida*, (now *G. fimbriaeplica*), *G. pantica*, *G. asclepiadea*, and the smaller more truly alpine endemic, *G. caucasica*. The tall blue thistle *Aethiopappus pulcherrimus*, much like a *Centaurea*, occurs just below the summit, so also the umbelliferous *Tommasinia purpurascens*, while on the top are *Dianthus cretaceus* (*liboschitzianus*), *Ranunculus caucasicus*, *Anemone narcissiflora*, *Helianthemum vulgare*, *Aconitum anthora*, *Primula cordifolia*, *Alchemilla vulgaris*, *Onobrychis oxytropoides*, a typical Armenian plant, *O. biebersteini*, the clover *Trifolium canescens*, and the two grasses *Koeleria fomini* and *K. phleoides*.

From the summit of Kochta a fine panorama is to be had of the nearby hills and of the glaciated high Caucasus Range to the north. The marked distribution of birch, beech, pine, and spruce is especially well seen in the view from the top of Kochta. The foliage tones delimit the zones well. An outline sketch of Kochta and the three mountain ranges to the north is diagrammatically given in Fig. 2.

From the summit of Kochta one may wander southward over the Kochta Hills (from left to right in Fig. 3) and find much the same sort of thing that the Kochta meadow offers, until one reaches the maximum altitude of 7875 ft. on the second of the three peaks. Here, within a very small area, a true alpine flora exists, exemplified by *Rhododendron caucasicum*, the tiny, prostrate, rosaceous *Sibbaldia parviflora*, and a Caucasian form of the composite *Erigeron caucasicus*. Three other species of *Campanula* occur here, *C. collina*, *C. aucheri* (flowering in June) and the delightful little alpine *C. tridentata*, so well adapted in form, above and below soil, for an alpine climate (Fig. 4).

<center>TZHRA-TZHARO[1].</center>

Zone I. The journey to the summit of Tzhra-Tzharo may be made via Kochta in the direction just described over the Kochta Hills, or better, by way of the Imeretin Hills on the opposite side of the basin. We shall go by this latter route.

The ascent of the Imeretin Hills is made from the north, consequently the lower forest is primarily of beech with very little spruce. The latter tree, though not over particular in regard to the points of the compass, is more at home on the west slopes. In the forests of the lower Imeretin Hills, *Fagus*

---

[1] Tzhra-Tzharo is a Georgian word, the pronunciation of which the Russians have retained by writing it "Zhra-Zharo." A *t* added to the *z* is the usual German transcription of the sound given to the letter *z* by the Russians; we usually write it *cz*, as in Czar.

Fig. 4. *Campanula tridentata*. (Drawn by Mrs M. S. Timofeev.)

orientalis attains its maximum size. Trunks 102 cm. in diameter are to be found (Pl. VIII, Phot. 7). Occurring with *Fagus* and forming equally fine boles is the elm, *Ulmus elliptica* (Pl. VIII, Phot. 6). The trunk of the elm is usually readily distinguished from that of the beech; the elm bark is rough and the beech smooth, but the difference in some cases is slight.

Wild pear trees occur in abundance on the edge of this lower deciduous forest. Whether the pears are to be regarded as *Pyrus communis* or *P. silvestris* is a matter of doubt. An occasional wild apple, *P. malus*, is also found.

Zone II. Again, as on Kochta, the beech is replaced by the maple at an altitude of 6500 ft. The last beech is passed at 6700 ft. *Acer trautvetteri* characterises this second zone, though the beech, birch, oak, and *Sorbus* occur, also the endemic *Rhamnus imeretina*.

Zone III. *Betula pubescens*, with *Sorbus aucuparia* and intervening subalpine meadows, make up the open forest association of the third zone on the Imeretin Hills (6700–7000 ft.). While the birch, as usual, forms the tree line here, *Sorbus* may, in places, climb higher. There is no pine; we are on the north slope.

Subalpine flowering plants make their first appearance in quantity here within the open spaces of the birchwoods. So far as the meadows are concerned, there is no line of division between these and the treeless ones immediately adjoining. Considered as a whole, the subalpine zone is made up of a lower portion of scattered birch trees with herbs and grasses on the open floor, and an upper portion of treeless meadows; it is, however, convenient to separate these two regions and to regard the tree line as a boundary delimiting the woods (and meadows) below from the fields above.

Zone IV. The subalpine fields (7000–8000 ft.) on the Imeretin Hills are rich in flowering plants, many of which are of those genera so typical of mountain pastures the world over: *Gentiana, Campanula, Primula, Geranium, Aconitum*, and *Trifolium*. Of these, the gentians are the same as occur on Kochta. Among the others there are two new campanulas, *C. steveni* and *C. aucheri*; two primulas, *P. ruprechtii*, and *P. pallasii*; one geranium, *G. platypetalum*; the endemic *Aconitum caucasicum*; and two clovers, *Trifolium ambiguum*, and *T. trichocephalum*. Other common species (not enumerated for Kochta) are *Lilium szowitsianum*, *Macrotomia echioides*, which gets up into the alpine regions, *Astrantia helleborifolia, Polygonum bistorta*, the umbelliferous endemic *Pastinaca armena*, the composite *Chamaemelum caucasicum, Linum hypericifolium*, the large weed *Agasyllis latifolia*, a *Hieracium, Anthemis rigescens, Tragopogon graminifolius*, two centaureas, *C. macrocephala, C. axillaris, Delphinium hybridum, Senecio platyphyllus, Valeriana alliariaefolia, Betonica grandiflora*, and *Eryngium giganteum*. Again there is present *Scabiosa caucasica*, the queen of them all, unless one wishes to give precedence to one of the most superb of poppies, *Papaver orientale*.

Zone V. The transition from subalpine to alpine flora is gradual until the high plateau of Tzhra-Tzharo is reached, where a pure alpine vegetation is

found. The alpine flora is of two main types, growing in equally distinct regions, (1) small herbs and low grasses on the wind-swept floor of the plateau, and (2) woody shrubs (*Rhododendron* and *Vaccinium*) forming thickets which cover the rocky precipices below the edge of the plateau.

The cold wind-swept top of Tzhra-Tzharo offers no protection to the more delicate alpine plants; they find better homes among the rocks over the edge of the plateau. Just before reaching the top, near the high mountain pass which leads over into Armenia, I collected an *Onobrychis*, *O. biebersteini* (*O. montana = O. sativa* var. *montana*). On the plateau, the most character-istically alpine plant is *Antennaria dioica*, which might well be called the "Bakuriani edelweiss" as Wulff has called *Cerastium biebersteini* the "Crimean edelweiss" and others *Anaphalis javanica* the "Javanese edelweiss." With *Antennaria* grows an equally typical alpine plant, the prostrate *Chamaescia-dium acaule*; this small umbelliferous alpine dweller was first collected on Tzhra-Tzharo in 1887 and has since been described for the Georgian Military Way and the north slopes of Mt Elbrus. The grasses which cover the high plateau are chiefly *Poa alpina* and *Festuca sulcata*.

The return journey to Bakuriani is more interesting if made down the north slope of Tzhra-Tzharo. Just over the precipitous edge of the plateau, protected from severe winds, a number of alpine plants, not yet mentioned, occur. Still to be found in flower during late August are *Astragalus incertus*, *Podanthum campanuloides* with its conspicuous steel-like spike, *Papaver mon-anthum*, and *Taraxacum crepidiforme*. (The region we are now in, is in the very centre of the upper half of the panorama in Fig. 3, just below the plateau ridge.) A true inhabitant of these alpine regions, not found with its relatives lower down, is *Campanula tridentata* (Pl. VIII, Phot. 8). This *Campanula* is one of the gems of the alpine flora. With it occur the little white-flowered *Saxifraga sibirica*, and an *Alchemilla* (Pl. VIII, Phot. 8). The latter is exceedingly abun-dant. Two likely species are *A. vulgaris* and *A. sericea*. Both of these are in doubt as are most alchemillas of the Caucasus. A new species of this genus, which is now in the hands of Mr Uzepchuk of the Leningrad Botanic Garden, was found on Tzhra-Tzharo.

Medicago gavahetica (also written *dzhawakhetica*) is a characteristic alpine plant of this region; it is endemic to the Minor Caucasus. Another member of this important Asiatic genus, also endemic at Bakuriani but not an alpine form, is *M. hemicycla*.

Slightly further down the precipitous north slope of the plateau, forming a broad belt the entire length of Tzhra-Tzharo, is a dense thicket of *Rhododen-dron caucasicum* with a more sparse intermixed growth of *Vaccinium uligino-sum*. The rhododendrons extend from 7000 ft. to the very rim of the plateau at 8800 ft.; the main growth of the belt is between 8000 and 8500 ft. altitude. One moss, *Polytrichum alpinum*, was gathered just below the rim of Tzhra-Tzharo.

Phot. 6. *Ulmus elliptica.*

Phot. 7. *Fagus orientalis*

Phot. 8. *Campanula tridentata* (centre), *Alchemilla* (back and right), *Saxifraga sibirica* (white flower, lower right) on Tzhra-Tzharo.

SEIFRIZ – SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA. III. PLANT LIFE IN THE BAKURIANI BASIN, MINOR CAUCASUS

Where the rhododendrons stop and the first birches begin on the north slope of Tzhra-Tzharo, a few scattered prostrate Junipers, *J. depressa*, are to be found.

MUCHERI.

The little knoll Mucheri (from the Georgian word *mucha* meaning oak; as so often happens in the case of names, there are no oaks on Mucheri) is the object of our next excursion. Mucheri has but one ecological fact to present, but presents that one so perfectly and vividly that it attains more prominence in a survey of the Bakuriani Basin than its size would otherwise justify.

On the south slope of Mucheri there is a pure stand of *Pinus hamata* and on the north slope there is chiefly *Fagus orientalis* (with some *Acer*, *Picea*, and *Pyrus*). This north-south distribution of beech and pine on Mucheri is so marked that the line of division runs down the precise centre of the east slope without a single specimen of the one or the other species encroaching on the opposite side of the line (Pl. VII, Phot. 5). In the Crimea there exists the same marked north-south distribution of beech and pine. The south slopes of the coastal Crimean mountains are forested mostly with pine (*P. silvestris*) while the north slopes are covered with a pure dense forest of beech (*Fagus orientalis*).

So thoroughly have pine on the south and beech on the north taken possession of Mucheri that little else grows there. Scattered specimens of *Populus tremula* and *Corylus avellana* occur in the underbrush (Pl. VII, Phot. 5). The former is a tree we have so far not mentioned in connection with plant life at Bakuriani; it is not abundant here as it is elsewhere in the Caucasus. *Corylus avellana* is a bush which attains a maximum height of 4 m.; it is more numerous at a lower altitude.

SHUGLIAT UBANI.

There remains but one mountain range to visit before completing the chain of hills which forms the Basin of Bakuriani; this is the Shugliat Ubani Range which lies to the north. (It is diagrammatically indicated in the foreground of Fig. 3).

At the base of the Shugliat Ubani we find the same trees which have been mentioned for the basin floor, beech, maple, oak, wild pears and apples. The slopes of the hills, which do not rise to great heights, are a pure stand of spruce and pine.

Rightly, these south slopes of Shugliat Ubani belong to the pine, yet spruce predominates. This is the only exception near Bakuriani of pine not forming a pure stand on the south slope. Spruce cannot compete with pine at higher altitudes, nor can pine successfully compete with spruce on the lower western slopes. The pine "prefers" light (the beech shade), but spruce shows little preference when mature, and may then predominate over pine, below

6500 ft. Where new ground is available, pine starts first. On Shugliat Ubani pure patches of dense growth of fine young pines may be seen. Once the trees are old enough to make shade, spruce will start and grow well, and there is no apparent reason why, once well started, the spruce should not persist and ultimately win out over the pine on south slopes.

Sorbus aria, characterised by my Russian friends as "wretched bushes, gnawed by cows," grows little at Bakuriani except on the south slopes of Shugliat Ubani. The only occurrence of the alfalfa, *Medicago hemicycla*, is also here.

OUTSIDE OF THE BAKURIANI BASIN.

The scarcity or absence of plants so typical of other similar and not far distant regions, is often strikingly brought to the attention of the ecologist. There is no plant more typical of Russian scenery than *Populus tremula*. It occurs throughout the lowland forests of Russia from Samara to the Arctic Circle; it clings to the tree lines in the mountains of eastern Turkestan, and forms the only stand of trees left at Kasbek, at 5600 ft., in the high Caucasus. We have mentioned this species as occurring at Bakuriani, but it plays no prominent rôle in the altitudinal distribution of plants there. The case is similar for the juniper.

The juniper is abundant in regions along the 42° parallel in the Soviet Union. It grows well as a tree on the coast of Crimea, occurs as a tree and as a low shrub throughout the high Caucasus, and forms striking large prostrate patches at high altitudes in the mountains of eastern Turkestan. In the Bakuriani Basin there are a few specimens of *Juniperus depressa*, and just over the rim of the basin, on the east slope of Kochta, Koslovski has located *Juniperus oblonga*; the number of specimens is not great. Koslovski has found another heretofore unreported plant from the Bakuriani region, *Cytisus ratisbonensis*; it is rather abundant, growing on rocky soil at 6000 ft. altitude in company with the juniper. It is with Mr Koslovski's kind permission that I publish the, as yet unrecorded, occurrence of these two plants near Bakuriani.

There can be but few places in the world which combine botanical interest and human appeal in so delightful a way as does Bakuriani.

DEPARTMENT OF BOTANY,
UNIVERSITY OF PENNSYLVANIA,
PHILADELPHIA, PA.

SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA

IV. AUTUMNAL PLANTS AT REPETEK, TURKMENISTAN

By WILLIAM SEIFRIZ.

(With Plates IX–XIII, and four Figures in the Text.)

THE desert of Kara Kum comprises the greater portion of the province of Turkmenistan in western Turkestan (Fig. 1). This waste area of "black sand" extends from the Caspian Sea on the west to the Amu Darya (literally, the Amu River) on the east, and from the Kopet Dag (the mountains which border Persia) on the south, to the Aral Sea on the north. The railroad from Krasnovodsk, the chief port on the eastern shore of the Caspian Sea, follows close to the Kopet Dag Range 100 miles beyond Ashabad, the capital of Turkmenistan. The journey eastward, from the Caspian to and beyond Ashabad, is through a narrow strip of clay desert land lying between the Kopet Dag Range and the desert of Kara Kum. It is sparsely inhabited and cultivated to some extent, being irrigated by streams fed from mountain springs. The people of this province, are Turkmen (pl. Turkmens), which is the correct Russian form for the perhaps better known English word Turkoman (pl. Turkomans). Their country is the Soviet Republic of Turkmenistan which reaches from the Caspian Sea to just beyond the Amu Darya.

One hundred miles beyond Ashabad the railroad turns to the north-east and crosses the south-eastern end of Kara Kum. Two oases are then traversed, the second being at Merv. From Merv the railroad passes through the desert 140 miles to the Amu Darya. Sixty miles more bring one to the city of Buchara, with Samarkand and Tashkent further to the east. Before the Amu Darya is reached, some 50 miles west of the river, one comes to the station of Repetek, one of the most centrally located railroad points in the Kara Kum desert (Fig. 1).

In early September, 1929, I had the pleasure of visiting Repetek in company with a number of Russian botanists, to whom I am grateful for many courtesies, especially our host, Dr M. P. Petrov, Director of the Station.

Repetek is a settlement of railroad officials and workers with their families. The total population of some seventy individuals, housed in six small buildings, is increased by three scientific men during the summer months. The station is without surface water. Two wells supply water of an indifferent (alkaline) quality. The usual household needs are supplied by transporting water by railroad. Irrigation is not possible.
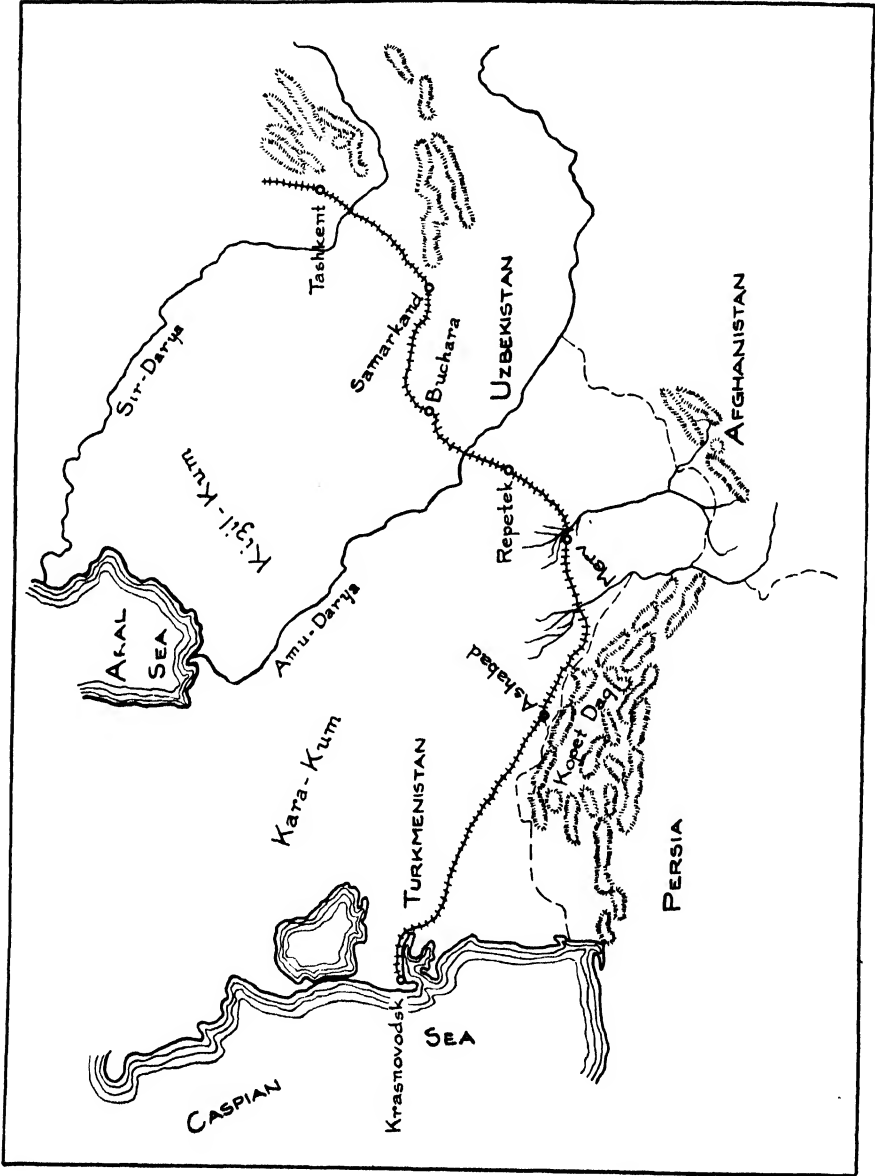
FIG. 1.

The desert at Repetek is of sand which the winds form into "barchans," giving to the surface that undulating topography which one commonly associates with deserts and which is in striking contrast to the flat clay desert land along the Kopet Dag Range, from the Caspian Sea to Ashabad in western Kara Kum. The billowy surface of the clean desert, embellished with scant but striking vegetation, gives to Repetek a most picturesque landscape which becomes all the more attractive in the early morning and late evening hours (Pl. IX, Phot. 1).

Repetek lies in latitude 38·5° N. and longitude 63° E. The climate is continental. The average July temperature in 1927 was 23·5° C. and in 1929, 31·8° C. A maximum shade temperature of 49·7° C. (121·5° F.) was reached in July, 1916. (A room temperature of 42° C. was recorded in the summer of 1928.) The sand surface becomes exceedingly hot, a maximum of 79° C. (174° F.) having been observed. This is a temperature which the plants must tolerate. The average January temperature is − 7·7° C.; the average minimum temperature for January, 1927, was − 22·5° C.; a January minimum of recent date (1928) is − 31° C. The annual range in temperature may therefore reach 70° C. (126° F.). Snow falls at Repetek but usually thaws in the daytime, though it may last a week or a fortnight.

In addition to the marked annual range in temperature there is also a pronounced daily range, especially in the autumn. It is not uncommon to have a temperature of 30° C. at noon, and of − 6° C. at 4 a.m. A diurnal range of 40° C., 30° C. in the day and − 10° C. at night, was reached in September, 1928. The low temperature is maintained only for about an hour in the early hours of the morning, consequently freezing seldom occurs. The daily range in temperature of the sand surface is naturally still greater. It may be more than 60° C.

Abolin[1] divides Middle Asia into eight temperature zones of which the hottest has an average summer temperature of 25° to 31° C. Repetek belongs to this zone. The continental climate of Repetek is further characterised by rainfall. The average annual precipitation is 94 mm., the average minimum, 24 mm., the average maximum, 170 mm. Rain falls only in winter. From May to September no precipitation occurs. In drought years there is no rain from April to December. The maximum number of days without rain so far recorded is 250, over 8 months. The minimum dry period is 131 days.

These two climatic features, a great annual range in temperature, falling well below freezing in winter, and a long summer period of drought, characterise the conditions for plant life at Repetek.

Before taking up the autumnal flora of Kara Kum as seen at Repetek, a word may be of interest in regard to the "barchans," as the distinctive sand

---

[1] **Abolin, R. I.** "Die Grundlagen des Naturhistorischen Rayonierens des Soviet Mittel-Asien," *Acta Universitatis Asiae Mediae*, Series XII a, Geographia, Fasc. 2, Tashkent, 1929 (in Russian with German summary).

dunes at Repetek are called (Pl. IX, Phot. 2). They are distinguished from true dunes by their movement and shape. Coastal dunes move constantly in one direction. Continental barchans move in one direction for half the year and then retrace their tracks the other half of the year; in other words, coastal winds prevail in one direction while continental winds reverse their direction twice a year. The winds at Repetek blow persistently from the north-west in summer and from the south-east in winter. The second factor distinguishing a barchan from a dune is shape. In profile the dune is curved, and the barchan straight. In plan, the dune is long with a small leeward end, and the barchan broad with a large deeply concave leeward end. The plan and profile of dunes and barchans are shown in Fig. 2 A and B; the seasonal positions of the barchans are shown in Fig. 2 C.

The total number of plant species to be found within a radius of a few miles of Repetek is 120 (130 with the fungi); of this number, about 25 are still to be found in September, and of these, 8 are annuals. The flora is thus characterised by two distinct groups of plants, a rich ephemeral spring vegetation and a scant winter one. This condition is due to the seasonal distribution of the rain; the total annual amount is sufficient to maintain plant life, but it is not distributed so as to carry the spring growth through the summer. In August and September only the dry skeletons of the spring ephemerals still persist.

Mr I. M. Vasiliev has demonstrated that at least some of these dry skeletons of the spring ephemerals are not dead. He has shown that *Carex*, sun-dried to crispness by natural winds—the leaves crumble to powder when crushed—will revive when artificially watered; the yellow and apparently lifeless leaves become green again.

Grasses and microphyllous shrubs characterise the autumnal plant life at Repetek. Of grasses, those still to be found in September are the endemic *Aristida pennata* with two varieties, *karelini* (Pl. IX, Phots. 3 a and b) and *minor*; *Bromus tectorum*, *Agropyrum orientale*, and *Schismus arabicus*. An adaptation (?) typical of psammophytes, and found well developed in *Aristida*, is the coating of sand on the roots which serves as an effective protection against desiccating winds when the roots become exposed. This coat of sand on the roots is rather typical of the Gramineae, and is not characteristic of all the desert plants. While the root hairs are probably in part responsible for the coating, there is some indication that it is primarily due to a glutinous exudation from the roots. This conclusion is supported by the fact that the coating of sand is thicker on the older parts of the root where no hairs exist. *Aristida* is further distinguished for its ability to maintain itself on the moving sands, whereas the other grasses mentioned persist only where the sand has become quiet and the barchan fixed.

A single *Carex* occurs; it is the endemic *C. physodes* with two varieties, *globosa* and *elliptica* (Pl. XIII, Phot. 11), distinguished, as the names indicate,

Phot. 3 a.

Phot. 3 b.

Phots. 3 a and b. *Aristida pennata var. karelini.*

Phot. 1. The desert at Repetek.

Phot. 2. The leeward end of a barchan.

SEIFRIZ—SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA. IV. AUTUMNAL PLANTS AT REPETEK, TURKMENISTAN
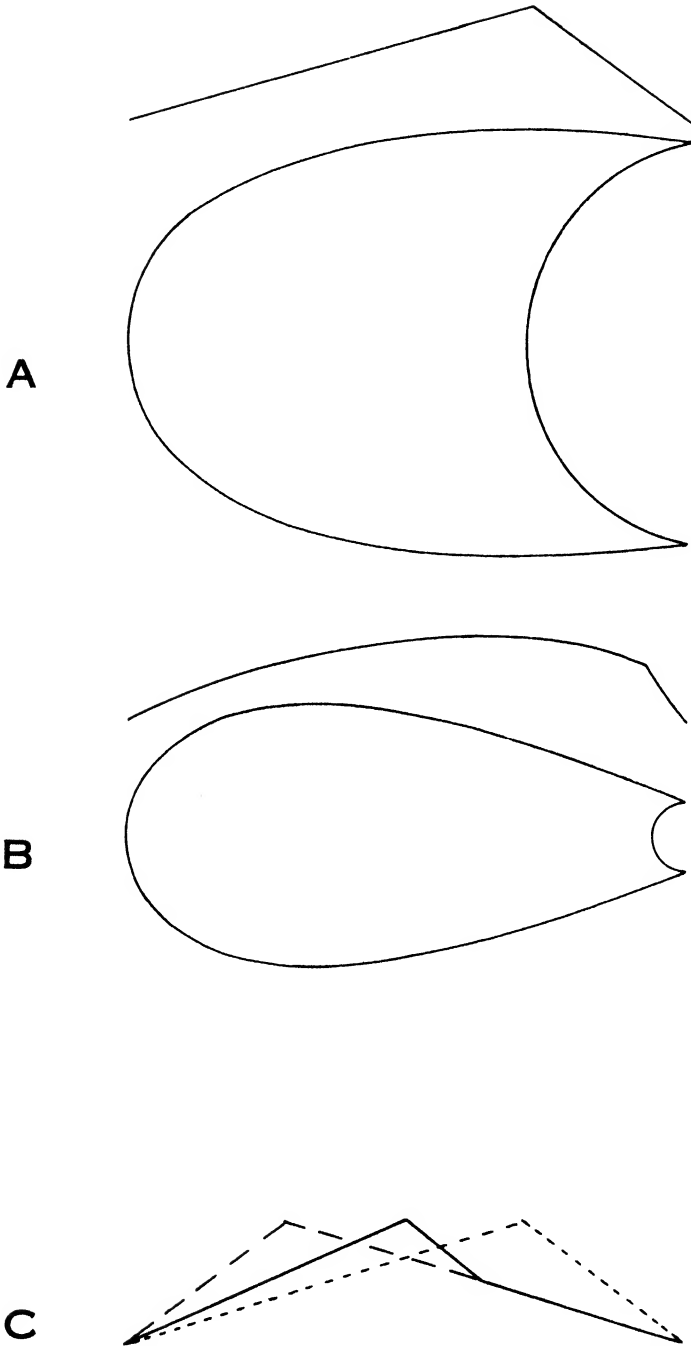
FIG. 2. A, Plan and profile of a barchan; B, of a dune; C, seasonal positions of a barchan: summer, dotted; winter, dash; spring and fall, solid line.

by the shapes of the fruits which are well adapted, in form and size, to rolling on the sand. *Carex physodes* is a plant of the sand deserts. It is replaced on the clay soils of eastern Kara Kum by *C. stenophylla*.

Salsola, so typical of all the south Russian deserts, steppes, and the sandy shores of the salt seas, is represented by two species, *S. richteri* with long narrow leaves (Pl. XIII, Phot. 11) and *S. subaphylla* with greatly reduced leaves (Pl. X, Phot. 4). The more renowned *Salsola kali* occurs on the clay deserts near the Aral Sea.

Among the legumes still growing in September are two species of *Astragalus*, *A. paucijugus* (*Ammodendron paucijugus*) and *Astragalus confirmans* (*A. ammodendron confirmans*).

Smirnowia turkestana is an interesting legume with attractive flowers and balloon-like fruits (Pl. XIII, Phot. 11) well adapted for wind dispersal. The spring leaves, which are about an inch long, are replaced by autumn leaves of not over three-eighths of an inch in length.

A characteristic of sand inhabitants, exhibited to a marked degree by a number of species growing at Repetek, is the formation of runners (Pl. IX, Phot. 3 b). Only an anatomical study can establish with certainty whether these are adventitious roots or stems (stolons). The majority of those observed at Repetek appear to belong to the root system. This is true of the runners of the borraginaceous *Heliotropium radula* which send up great numbers of shoots (Pl. XI, Phot. 7). *H. dasycarpum* is another species of this genus occurring at Repetek. The runners of *Eremosparton flaccidum* and of the tree-shrub *Ammodendron conollyi* are stolons.

The five species of *Calligonum* (Polygonaceae) form a characteristic group among the desert plants at Repetek. Most typical is the small *Calligonum caput medusae*, var. *rubicunda*; it is very abundant, with a profuse root system often laid bare by the winds (Pl. X, Phot. 5). *Calligonum setosum* and *C. comosum* are less abundant. Two tree-like forms of this genus are the endemic *Calligonum arborescens* and the 20 foot *C. eriopodum* (rare at Repetek). All the Calligonums are leafless.

Four other arborescent shrubs occurring at Repetek are the two legumes, *Ammodendron conollyi*, which is common, and the leafless *Eremosparton flaccidum*, a tree shrub reaching seven feet or more in height, with functional cladodes; and the two Chenopodiaceae *Arthrophytum arborescens* and *A. haloxylon* (*Haloxylon ammodendron*) which form fine tall clumps scattered here and there in the desert (Pl. XII, Phot. 9). Two smaller Chenopodiaceae are the spiny *Horaninowia*[1] *ulicina*, which is abundant (Pl. X, Phot. 6), and *Agriophyllum latifolium*.

Ephedra alata is a characteristic but not abundant species at Repetek (Pl. XI, Phot. 8).

---

[1] The *w* in this name is also written *v*.

Phot. 5. *Calligonium caput-medusae.*

Phot. 6. *Horaninovia ulicina.*

Phot. 4. *Salsola subaphylla.*

SEIFRIZ—SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA. IV. AUTUMNAL PLANTS AT REPETEK, TURKMENISTAN
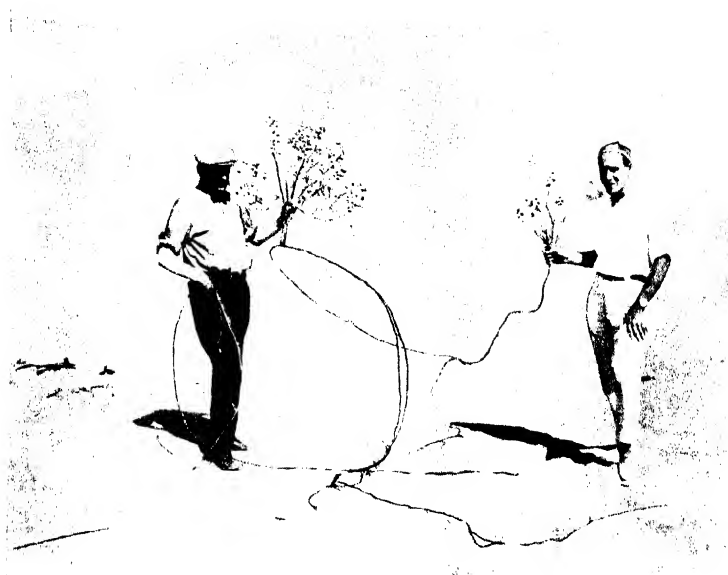
Phot. 7. *Heliotropium radula.*

Phot. 8. *Ephedra alata.*

SEIFRIZ　SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF
SOVIET RUSSIA. IV. AUTUMNAL PLANTS AT REPETEK, TURKMENISTAN

Alhagi camelorum, the outstanding plant of the clay deserts of Turkestan, occurs at Repetek as a weed but it is not typical of the sands, being an escape from the adjoining clay deserts which border the Caspian Sea on the east, lie at the foot of the Kopet Dag Range on the south and make up much of the
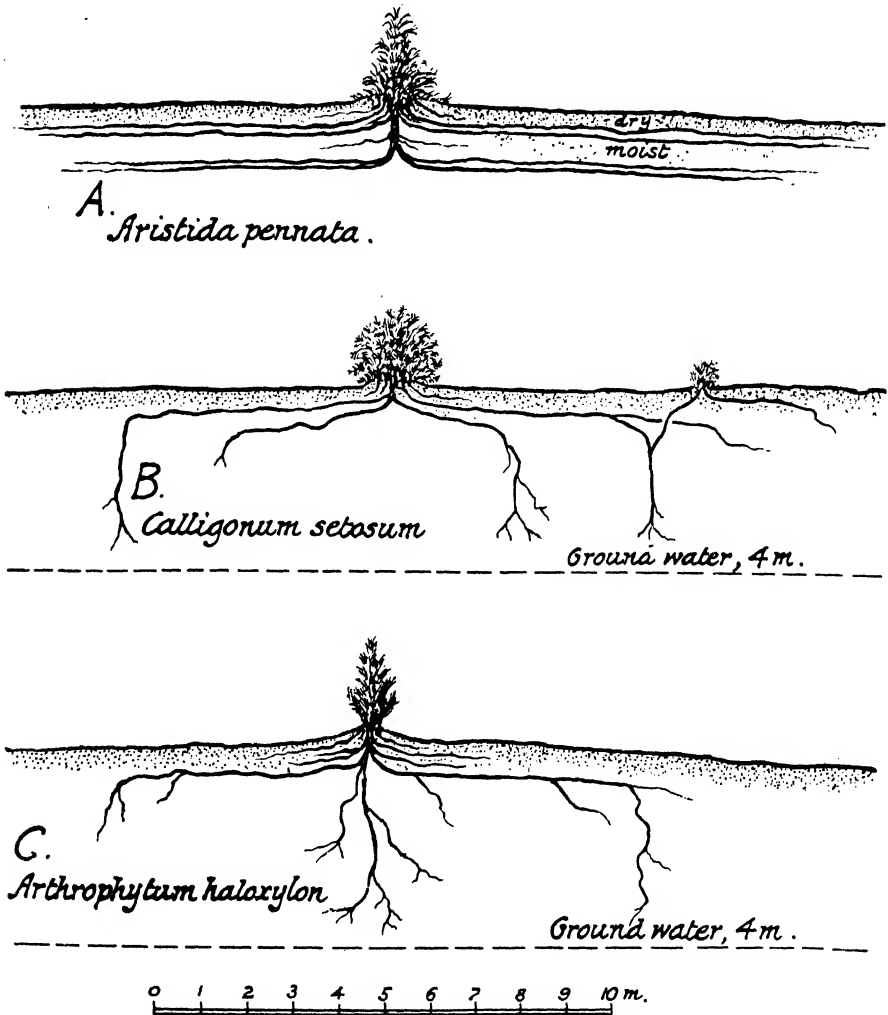
FIG. 3. Root systems (modified from M. P. Petrov, and drawn by Paul Bausch).

Kizil Kum desert to the north from Tashkent to the Aral Sea. Throughout this extensive area *Alhagi camelorum* forms the chief food of the camel (Pl. XII, Phot. 10). This legume is eaten by no other grazing animal because of the slender, sharp spines. The tiny pods hang from the spines (Pl. XIII, Phot. 11).

The fruits to be found at Repetek make an interesting and attractive

collection (Pl. XIII, Phot. 11). Especially fine are the hairy, sometimes spiny spheres of the Calligonums, which are of considerable variety.

The ecological and physiological problems which plant life at Repetek presents are many. A prolonged stay is necessary to attempt even a superficial study of them. One of the most interesting of these problems is that having to do with the types of root systems. The Director of the Repetek Station, Dr M. P. Petrov, has made an intensive study of the root systems of the psammophytes growing there. It is with his kind permission and the generous
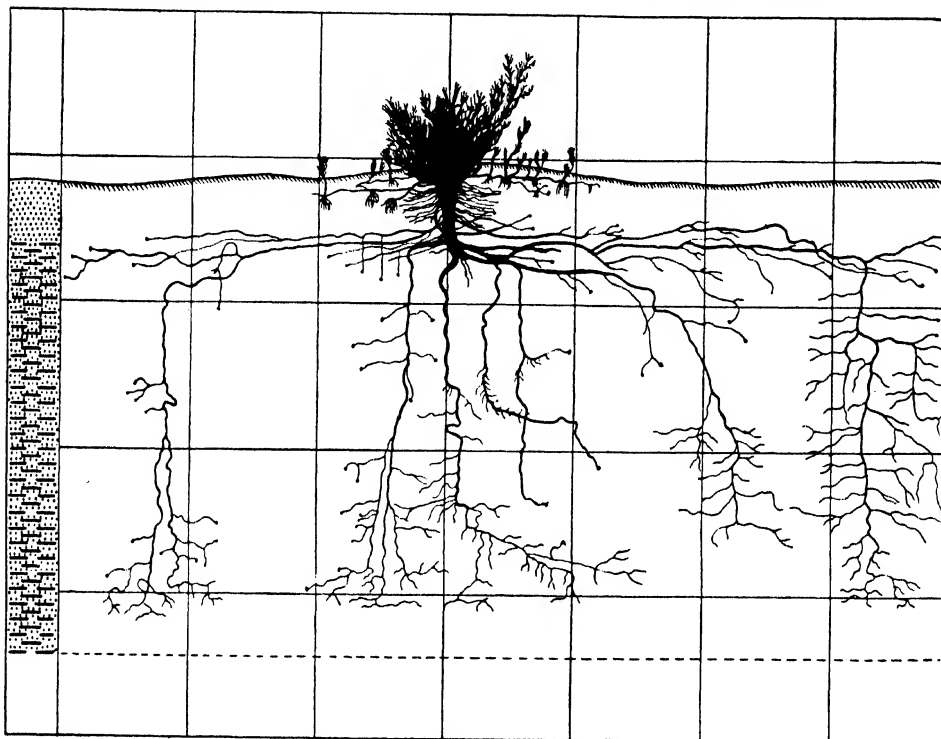
Fig. 4. Root system of *Ephedra alata* (from M. P. Petrov); the side of a square is 1 m., the dotted line is ground water; soil column at left, dotted area is eolic sand, dash is gray alluvial sand.

help of Mrs Irena Vladimirovna Krassovsky, also known for her studies on root systems, that I give here some of the results of Dr Petrov's work[1] and republish one of his illustrations.

Three main types of root systems are represented among the Repetek psammophytes. The members of the first type, among which *Ammodendron, Eremosparton* and *Aristida* are the outstanding examples, make up the advance guard, so to speak, in that they subsist on the moving sands. Their roots spread to great distances near the surface, but they keep below the first 40 cm. of

[1] "Root systems of the principal psammophytes of the sand desert of Kara Kum, *Bull. Applied Bot.*, Leningrad, 1930.

Phot. 9. *Arthrophytum haloxylon.*

Phot. 10. *Alhagi camelorum* on the northern clay desert steppes near the Aral Sea.

SEIFRIZ—Sketches of the Vegetation of some Southern Provinces of Soviet Russia. IV. Autumnal Plants at Repetek, Turkmenistan

dry sand and within the next 150 cm. of moist sand, below which dryness again prevails (Fig. 3 A).

The members of the second type, of which *Calligonum setosum* is an example, are found on quiet and not yet well cemented sands. Such plants develop a short main root with long lateral roots, which first grow horizontally for some distance and then turn downward, reaching ground water at a depth of 3 to 4 m. (Fig. 3 B).

The third type, represented by *Arthrophytum haloxylon* and *Ephedra alata*, is found on quiet, thoroughly cemented (and salty) sands; the main root is well developed with very small lateral roots near the surface; the root system is thus adapted for utilising both the surface water from spring rains and the ground water at a depth of 4 m. (Fig. 3 C). Very substantial horizontal roots with deep vertical extensions, which may reach ground water, are also formed. Dr Petrov has illustrated this type in the case of *Ephedra alata* (Fig. 4) where the main root is less definite than in *Arthrophytum haloxylon*.

The soil at Repetek is diagrammatically represented at the left side of Fig. 4: the upper layer, $\frac{1}{2}$ m. deep, is of eolic sands; the lower depths are all gray alluvial sands down to ground water (marked by the dotted line) at $3\frac{1}{2}$ m. The water table is at a constant level of 3 to 4 m. measured between the barchans, which is a considerably less depth than in the most favourable situations of the deserts in the southern and western United States.

Artemisia, which is so familiar a plant throughout the extensive Russian and Turkestan steppes, is wholly lacking at Repetek, where plant life is more distinctive than in any of the five regions described in this series of articles.

DEPARTMENT OF BOTANY,
UNIVERSITY OF PENNSYLVANIA,
PHILADELPHIA, PA.

SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA

V. THE PLANT LIFE OF THE TRANSILIAN MOUNTAIN RANGE IN SEMIRECHJE, EASTERN TURKESTAN

By WILLIAM SEIFRIZ.

(With Plates XIV–XVI, and two Figures in the Text.)

THE present article is the last in a series of five dealing with plant life in the southern countries of the Union of Soviet Socialistic Republics. My part in the work which has led to the writing of these articles was merely to collect the plants, note their localities, and assemble all facts for publication. The final identification of the species, which constitutes the foundation of any geographical or ecological study, has been done by Russian specialists residing in the respective countries. To them do I again express my appreciation not only for the botanical information received but for their delightful hospitality.

The identification of the plants collected in the Transilian Mountains and described in this article was done by Mr Alexis Vvedensky of the Botanic Institute of the Middle Asiatic University at Tashkent; my thanks are due to him for this courtesy.

The Transilian (Zailiiskii) Range is the last, to the north, of that massive group of mountains which rests on the borderland of Afghanistan, Kashmir, China, and Turkestan (Fig. 1). The Russian part of this territory includes, from south to north, Pamir, Ferghana, Tian-Schan, and the Transilian Mountains. These last lie in the old province of Semirechje which is now the southern part of the new Kazak[1] Republic.

The official designation of Kazakstan is Kazak Autonomous Soviet Socialistic Republic or Kazak A.S.S.R. The "republic," when formed shortly after the revolution, consisted only of the old Russian province Semirechje, but it has since been extended to include all of the vast steppe which lies to the north as far as the trans-Siberian railroad. The eastern and southern boundary of Kazakstan is Chinese Turkestan. On the west is Uzbekistán.

Semirechje is generally assumed by Russians to mean "Seven Rivers" (literally "Seven Little Rivers") in reference to the seven rivers which flow into Lake Balhash. There is, however, a legend which states that "rechje" is

---

[1] Kozak and Kazak are forms of the same Tartarian word meaning "rider"; both are used to indicate a cossack. Etymologically the two words are identical, but ethnologically the kozaks (cossacks) of the Don and the Kazaks of eastern Turkestan have nothing in common.
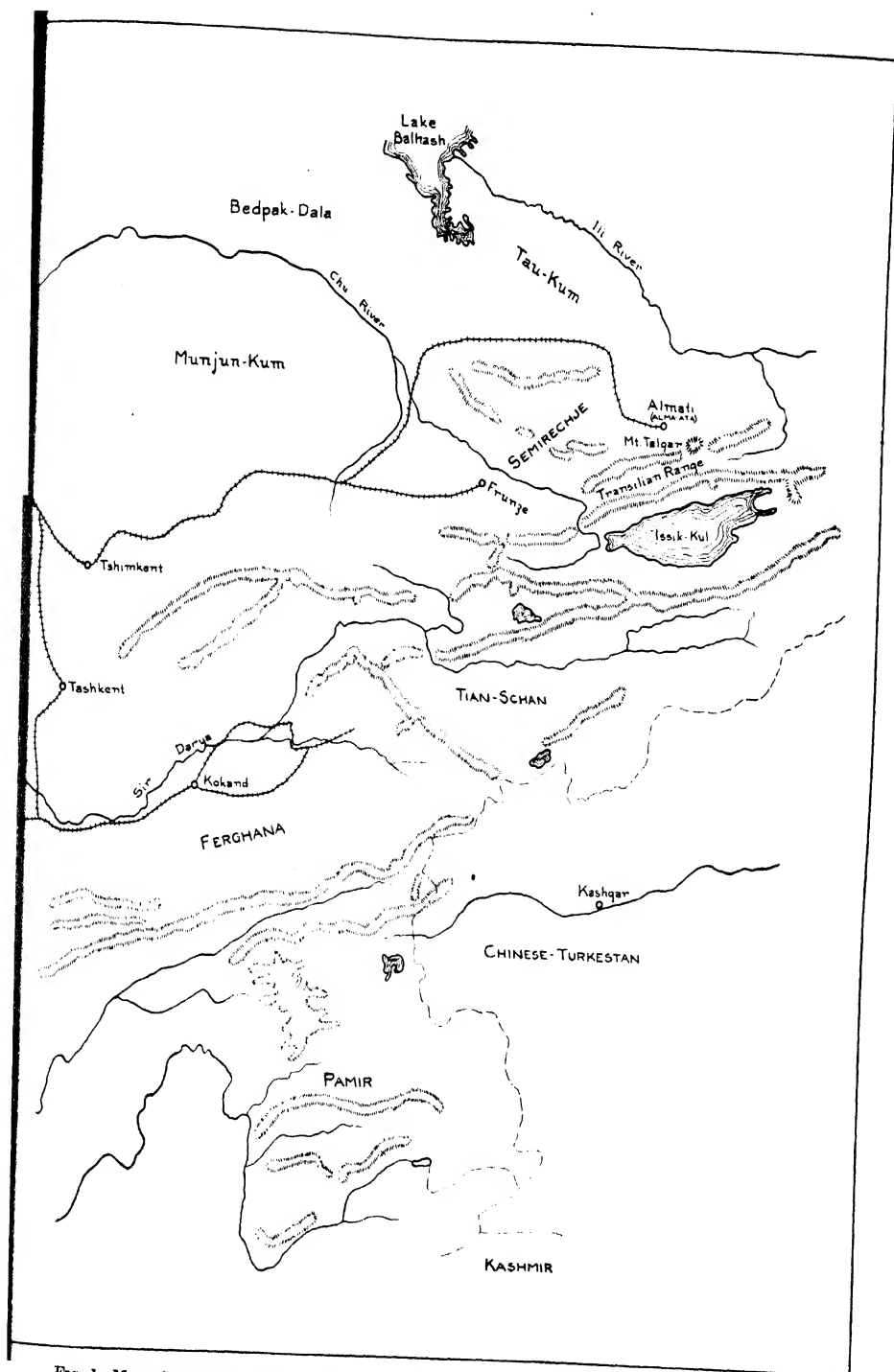
FIG. 1. Map of eastern Turkestan including the southern part of Kazakstan. Almati and the
Transilian Mountains lie in the upper right corner.

a changed derivative from a word meaning "little farms"; if this is true, then Semirechje becomes "Seven Little Farms."

The inhabitants of Semirechje are Kirgizi and Russian immigrants. To the Russians, all the natives are Kirgizi, but the latter have adopted and demand the official, as well as racial, distinction between the Kazaks (Kirgizi of the better class) and the Kara (Black) Kirgizi. To the casual observer visiting the country the population is almost evenly divided between the Kirgizi (Kazaks and Kara-Kirgizi) and the Russian settlers. A few Dungani, Mongolian immigrants, live close to the Chinese border.

Kasakstan comprises a narrow southern mountainous region, including Tian-Schan, and an extensive flat territory to the north and west; this last is mostly steppe (Bedpak-Dala, or "Hunger Steppe"), and the rest desert (Mujun-Kum). Lake Balhash (or Balkash) lies in the southern sandy part of Kazakstan, not far north, as Russian distances go, of the Transilian Range which we are to visit. The Ili River, the largest of the seven rivers which flow into Lake Balhash, rises in China, flows due east, to a point north of Almati, and then bears north-west to the lake. From it the Transilian Mountain Range derives its name.

The capital of Kazakstan is Almati (or Alma-ata) (Fig. 2). It is 150 miles from the Chinese border on the east. Almati is a primitive town with poor accommodation unless one has the good fortune to enjoy the hospitality of a Russian household. Verni (Vjerni), the "Faithful," was the name of the old Russian fortress there, and by this name did the place go in pre-war days. A still earlier name of the town was Alma-ata, "Father of Apples." This name was adopted by the Soviet Government after the revolution, but has since been changed to "Almati."

Almati is well called "Father of Apples," for not only is the wild apple very abundant there, but the cultivated ones are exceptionally fine in taste, and huge in size, a diameter of 5 in. being not uncommon.

The Transilian Mountain Range is about 75 miles long extending in an almost east to west direction along the 43rd parallel. The 77th meridian passes through the centre of the Range. The mountains rise to a maximum height of 4856 m. (15,927 ft.), which is the altitude of Mount Talgar (this is the latest official figure; another Russian value is 4267 m.; recent German maps record the height as 4570 m.). The Range is glaciated throughout its length. A number of excellent excursions of from one to five days' duration can be made into the mountains from Almati. Once well within the Range one is forced to travel without trails except for chance ones made by sheep. Apparently, none of the higher peaks have been ascended. Relatively little of the country is known to others than herders. Information is vague and uncertain.

An interesting and thoroughly delightful one or two-day trip is that from Almati up the small Almatinka River to the glacier. Just beyond, on the south side of the Transilian Range, is Lake Issik-Kul (Fig. 1).

PURE STEPPE

SALT-SAND STEPPE

WET-SALTY MEADOW

FERTILE SAND-LIME SOIL

MEADOW-STEPPE

SPRUCE FOREST & SUBALPINE MEADOWS

HIGH-ALPINE MEADOWS

ETERNAL ICE
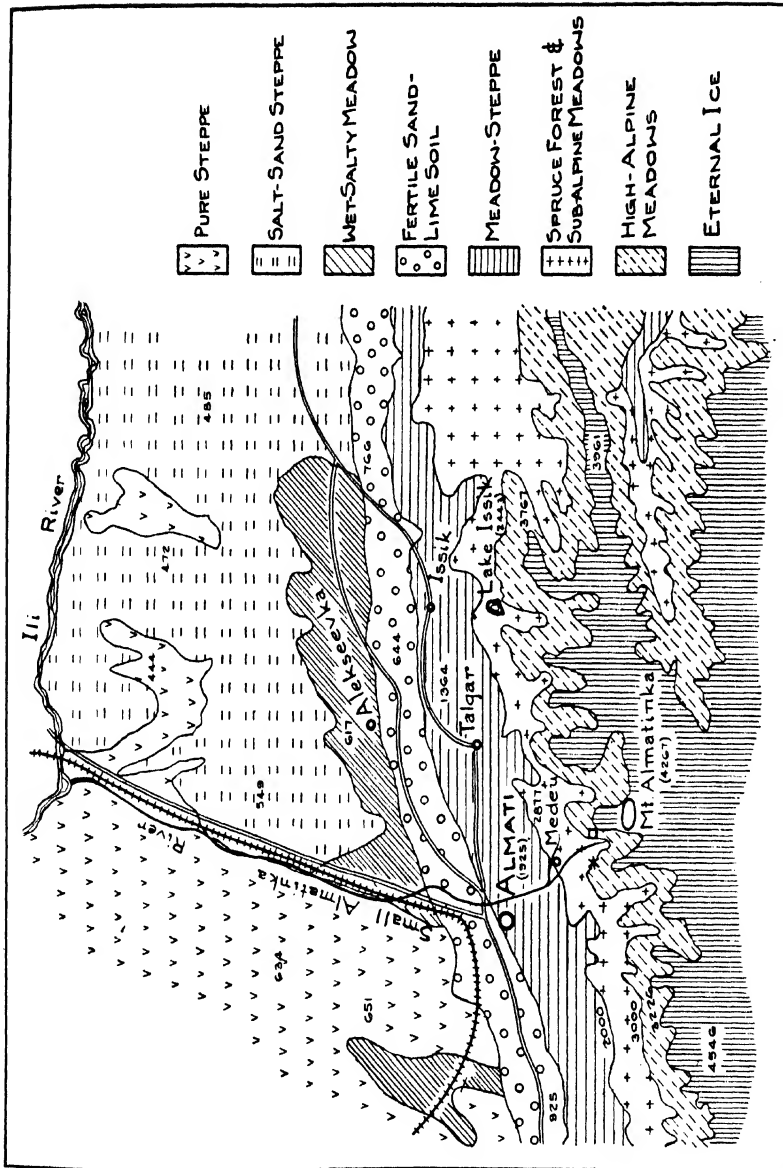
FIG. 2. Map of the Almati district, being the upper right corner of Fig. 1. The Small Almatinka River runs north from the glacier of Mt Almatinka and then follows the road from Almati to the Ili River. Mt Almatinka is marked with an oval. Medeu is indicated by a small circle near the head waters of the Small Almatinka River. The alpine summit in Pl. XVI, Phot. 8 is marked with an asterisk, and the rocky peak in Pl. XVI, Phot. 9 with a square. Issik village is 30 miles east of Almati. Lake Issik lies in the mountains south of the village. The large lake, Issik-Kul, shown in Fig. 1, is just off the map to the south. (Slightly modified after Abolin.)

A longer trip, requiring at least five days to carry out properly, is from Almati to Issik by carriage, then on foot or on horseback to the Issik lakes above and beyond; from here daily excursions can be made into the mountains. This latter trip, though painfully dusty across the steppe in dry weather (during August and September), is well worth the bother because of the beauty of the mountains and lakes, and the diversity of the vegetation. I shall first describe this journey and then tell of the vegetation in the Small Almatinka River valley.

The little village of Issik lies 30 miles east of Almati (Fig. 2). A full day is needed for the trip if one travels by wagon with the usual horses available. From Issik to the mountain lakes is another three or four hours' journey. One may divide the trip across the plains, from Almati to Issik, into two parts of a day each, or travel through to Issik and spend the night there. In the former case the night is passed at a caravanserai at Alekseevka or Talgar; in the latter, one is forced to ask permission to partake of the hospitality of a peasant at Issik. The one-room mud hut of the peasant will accommodate three more in addition to his family of five. In either journey one may have tea from a samovar and simple food such as bread, milk, eggs, honey, and blini (pan-cakes). It is, however, always advisable when travelling in Russia to have an emergency supply of food, and, of course, in the mountains one is entirely dependent on one's own rations.

The journey from Almati to Issik is across typical Siberian steppe (Fig. 2 and Pl. XIV, Phot. 1). The land is flat, the soil loess. The altitude of Almati is 841 m. and of Issik 950 m. Precipitation is ample, 576 mm. annually at Almati, and seasonally well distributed. The land to the north of the road is a vast steppe extending to Siberia. To the south, i.e. between the road and the mountains, the land is fertile meadow steppe with scattered small trees, the most abundant among them being "Karagach," *Ulmus campestris* (formerly so called, the species is now in doubt). *Populus tremula*, a species of *Salix*, and an occasional small oak also occur. The oak has been introduced; it is not native here.

The vast expanse to the north, part desert and part steppe, is characterised chiefly by *Artemisia*, the most abundant species of which, bordering the Transilian Range, is *A. terrae albae*. *A. sublessingiana* also occurs. Grass steppes are intermixed with the *Artemisia* ones; in the former, *Stipa capillata* usually predominates, though *Festuca sulcata* and *Stipa lessingiana* may, in places, be more typical. The *Artemisia* steppes harbour a number of other plants, among which the composite *Chondrilla* grows in abundance. The latter plant is receiving much attention from the Russian government as a possible commercial source of rubber. *C. brevirostris* predominates in the sandy plains. The genus gets up into the mountains, where *Chondrilla pauciflora, C. ambigua* and *C. coronifera* occur.

Atriplex verrucifera is also typical of the *Artemisia* steppe. Less characteristic though very abundant are the composite *Onopordon* and the tall

PLATE XIV

Phot. 1. *Artemisia* steppe (with Kirgizi huts) north-west of Almati.

Phot. 2. Lake Issik (2443 m.).

Phot. 3. *Ephedra procera* at Lake Issik.

SEIFRIZ — SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA. V. PLANT LIFE OF THE TRANSILIAN MOUNTAIN RANGE IN SEMIRECHJE, EASTERN TURKESTAN

grass, *Phragmites communis*. It is through such a dreary waste, dotted here and there with Kirgizi huts, that one passes in journeying from Almati to Issik.

The village of Issik, at an altitude of 950 m., lies close to the Transilian Mountains. The foot hills of the range are bare of trees. Mountain meadows characterise the lower hills from Tashkent to Issik. Occasionally the hills are forested but then only with second growth, as within the Small Almatinka River valley, where *Populus tremula* forms pure stands. The absence of an arboreal vegetation on the foot hills is probably due to cutting many years ago.

From Issik, the trail leads south, following the headwaters of the Issik River, into the gorge at the upper end of which lie the mountain lakes which are our goal. Once out of the hot dry steppe and well within the cool moist confines of the gorge, *Malus communis* is met with in great numbers. This wild apple forms small woods to the almost complete exclusion of other trees.

Crataegus first occurs in the gorge and continues up into higher regions. The tree shrub *Prunus padus* is limited to lower levels. The black maple, *Acer semenovii*, with very small leaves, is an interesting inhabitant of the lower mountains, but it is not abundant.

Among the shrubbery and herbaceous undergrowth of the gorge are *Berberis heteropoda*; *Rosa beggeriana*, with small white flowers and red pear-shaped fruits (*Rosa pimpinellifolia* with smaller leaves and spherical fruits will be met with higher up); *Ribes (nigrum)*; *Euonymus semenovii* with its pink carpels, brilliant red seeds, and yellow arillus, is conspicuous and abundant; *Potentilla reptans*; the ubiquitous *Cichorium intybus*; and three attractive Althaeas, *A. nudiflora, A. rhyticarpa* and *A. litvinovii*. The last of these three Althaeas is a newly recognised species; it is a hybrid between *nudiflora* and *rhyticarpa*. Another member of this family (Malvaceae) is *Lavatera thuringiaca* with pale rose-coloured flowers, so much like an *Althaea* that the uninitiated would mistake it for the latter; the difference lies in the number of "Nebenblätter," three in *Althaea* and six in *Lavatera*.

Very abundant in the gorge, and at first thought an apparent escape from the steppes, is *Artemisia*. This genus is of extraordinarily wide distribution. The species here is *A. absinthium*; the one most typical of the steppes is *A. terrae albae*; at a higher altitude (1600 m.) we shall meet with *A. annua*. Abolin uses the pronounced vertical distribution of *Artemisia* to point out that an account of the altitudinal distribution of plants is not as simple as is usually presumed; thus, typical *Artemisia* steppes occur at 200, 1200, 2200 and 3200 m. Altitude in itself, i.e. a reduction in atmospheric pressure, can hardly be a deciding factor. It is the climatic conditions determined by altitude which affect the type of flora. One of these is precipitation, but it apparently follows no fixed rule in relation to altitude, as assumed by Schimper and others. Localities may be of nearly the same altitude and yet have markedly different precipitations; thus Galmenhorn, in the Swiss Alps, at an altitude of 2850 m.,

has an annual rainfall of 670 mm., while Seewinenberg, of very nearly the same altitude, 3025 m., has 3170 mm.

Schimper thought that precipitation increased up to a certain altitude and then decreased owing to the lessened vapour content of the air, but Abolin shows that this rule does not hold for regions in Turkestan, where there may be a steady decrease in precipitation with increase in altitude. Abolin presents his evidence in the following table.

	Altitude (m.)	Precipitation (mm.)
Alma-ata	841	576
Karakol	1770	431
Marin	2015	266
Irkeshtam	2850	164
Pamir	3640	59

High *Artemisia* steppes do not occur in the Transilian Mountains to the extent that they do on the plateaux (3000 m.) of Pamir, and Central Tian-Schan. However, *Artemisia* occurs in abundance in the subalpine and alpine meadows of the region we are visiting, reaching an altitude of 2500 m.

In old botanic, geographic, and even in pure taxonomic works, the Artemisias are put into one species, *maritima*, described by Linnaeus for the Baltic shores. The taxonomists now divide this species into a number of varieties and even into good species which are morphologically distinguished only by minor characters but geographically are definitely distinct by the fact that they are limited to certain localities, i.e. to altitudinal belts. Abolin[1] describes *Artemisia turanica (turkestanica)* as characteristic of the salt steppes of the Balhash Lake region which adjoins the Issik-Almati desert steppe on the north. Nearer to the mountains, this species is replaced by *A. terrae albae*, and in the foot hills, by *A. sublessingiana*. The *Artemisia* steppes of the inner mountain valleys of eastern Turkestan harbour a special group: thus, in Central Tian-Schan the *Artemisia* approaches *A. lehmanniana*. On the high mountains of Tian-Schan the steppe is made up of the very characteristic *Artemisia rhodantha*, and in Pamir by another typical species, *A. skorniakovii*. Abolin believes that the geographic paradox which puts one *Artemisia* species at all altitudes is solved by realising that the plants are not of the same species. While it is well to emphasise the anatomical differences which a genus exhibits when growing at different altitudes, the origin and permanence of the differences must be the deciding factors in the determination of the species. *Artemisia* "species" may be true genetic, and therefore taxonomic, ones, or they may be variable expressions of the environment. The extraordinary change in form which plants are known to assume with change in environment, forces one to recognise that change in environment due to change in altitude may be responsible for the variations in *Artemisia*. Before coming to any final

[1] **Abolin, R. I.** "Die Grundlagen des Naturhistorischen Rayonierens des Soviet Mittel-Asien," *Acta Universitatis Asiae Mediae*, Series XII a, Geographia, Fasc. 2 (Tashkent), 1929.

conclusion in regard to the *Artemisia* species it would be well to observe if the differences persist in another habitat.

The tree which distinguishes the mountain forests of all eastern Turkestan is *Picea schrenkiana*; we meet it here in the gorge at its lowest altitude.

The first and smaller of the two lakes nestles at the foot of a rocky precipice close to the edge of a massive natural dam at the head of the gorge. A quarter of a mile farther on, is the larger of the two lakes. Like a huge piece of malachite it rests in its setting of spruce-covered hills and snow-capped mountains (Pl. XIV, Phot. 2). A forester resides at the second lake and an additional hut provides shelter for visitors. Wild game abounds. The region is under government control, as are now all of Russia's forests.

Once the lakes are reached at 2443 m., a subalpine flora prevails. The forests, of rather open formation, are almost pure *Picea schrenkiana*.

Another Gymnosperm occurring in these mountains, though quite a different sort of plant from *Picea*, is *Ephedra procera*, which, though not abundant, forms some very good clumps (Pl. XIV, Phot. 3).

Small groups of *Populus tremula*, some scattered *Sorbus* and an occasional *Malus* occur, the last rather out of its natural environment, escaped from its home below. *Picea* forms the tree line at 2600 m., though *Populus* climbs high.

A small-leaved mountain birch, *Betula songorica (tianschanica)* is found, but it does not grow in great numbers. The taxonomists are not prepared to name with certainty any birch from this region. Fedchenko, the recognised authority on the flora of Turkestan, says, "To distinguish definitely the Turkestan birches is at present quite impossible." A *Salix* also occurs.

The little *Prunus prostrata* of but 2 or 3 ft. in height is interesting; it occurs not infrequently at this altitude (2500 m.) though more common on the lower mountain slopes.

Crataegus is abundant. In the journey from the Crimea to eastern Turkestan by way of the Major and Minor Caucasus, this genus is met with at all lower altitudes. The small tree *Lonicera microphylla* is characteristic of this region. *Spiraea hypericifolia* grows in great profusion. A second species of *Rosa*, *R. pimpinellifolia*, with spherical fruits and leaves smaller than those of *R. beggeriana* at a lower altitude, is exceedingly abundant here. These four genera, *Crataegus*, *Lonicera*, *Spiraea* and *Rosa* are typical of all the eastern Turkestan Mountains, a fact further emphasised by Raikovas' mention of them to characterise the north, wet, mountain slopes of Pamir in contrast to the south, dry, grass slopes where *Stipa* predominates.

Rubus idaeus, *Berberis* and *Cotoneaster* occur not uncommonly, as also the following herbaceous plants: *Rheum*, an escape from the lowlands; *Origanum vulgare*, a Labiate which is equally abundant lower down; *Turritis glabra*, an unusual genus with but a single species in Russia; *Patrinia intermedia*, a rare member of the mountain flora; an *Erigeron*; *Ligularia macrophylla*; *Atraphaxis frutescens* with attractive small pink fruits like its better known relative

Rumex; the red-flowered *Althaea rhyticarpa* and *Lavatera thuringiaca*, both escapes from the lowlands, as is also a *Ribes (nigrum)*; *Echinops karatavicus*; *Impatiens parviflora*; a *Lathyrus* species; *Hieracium virosum*; *Echium vulgare*; *Senecio jacobaea*; and *Trifolium pratense*.

Ferns are not numerous, though good patches of the crisp and world-renowned *Polypodium vulgare* are to be found on cliffs.

Mosses are more abundant here than in any of the mountainous regions visited by me in southern U.S.S.R. The following have been kindly identified by Mr R. S. Williams of the New York Botanical Gardens:

Distichium capillaceum	Abietinella abietina
Didymodon rubellus	Tomenthypnum nitens
Tortula montana	Brachythecium trachypodium
Mnium rostratum	Hypnum bambergeri
Plagiopus oederi	H. imponens
Orthotrichum rupestre	Rhytidiadelphus triquetrus
Pseudoleskeella catenulata	Hylocomium proliferum

Stone encrusting lichens occur in profusion. Most abundant is *Lecanora rubina*. The following additional species were also collected and have been kindly identified by Prof. C. C. Plitt of the University of Maryland.

Lecanora subfusca	Peltigera horizontalis
Lecidea (Biatora) sp.	Letharia divaricata
Cladonia pyxidata neglecta	Gyrophora spodochroa
Parmelia sulcata	

Climbing 200 m. above the lake one comes upon the first indication of an alpine vegetation. On the north slopes *Picea schrenkiana* climbs to the crest of the lower mountains (2600 m.). On the south slope the spruce is wholly lacking. The marked adjustment of *Picea* to the north and south slopes is to be better observed in the Small Almatinka Gorge which we shall next visit.

The only woody plant reaching the alpine zone on the south slope above the lake is *Juniperus sabina (polycarpos)*. More characteristic of these mountains as a whole and occurring in great abundance on the Almatinka Hills, is *Juniperus pseudosabina (turkestanica)* a typical prostrate juniper. *J. sabina* often rises several feet above the ground when an old specimen has developed a thick, twisted, gnarled trunk.

The slopes and summits of the lower surrounding hills rising 200 m. above the lake (to an altitude of 2600 m.) are pastures that harbour an essentially subalpine flora, with, however, an occasional indication of an alpine character. To reach a pure alpine vegetation one must climb to 2800 m., as we shall do in the Little Almatinka region.

Of chief interest in the subalpine fields above the lakes are two *Artemisia* species, the small leaved *A. annua*, typical of the mountains, and *A. absinthium*; both occur in abundance, though the latter species is more typical of the lower hills. The last flowers of a gentian still persist; two Silenes are in fruit, one of them *Silene venosa* (a synonym of *S. inflata* apparently used to distinguish the Russian form from the European one); *Polygonum alpinum*;

Phot. 5. A pure stand of *Picea schrenkiana.*

Phot. 7. The marked restriction of *Picea schrenkiana* to northern slopes.

Phot. 4. *Picea schrenkiana* in the Small Almatinka Valley.

Phot. 6. *Picea schrenkiana* and, in the foreground, the prostrate *Juniperus pseudosabina (turkestanica)* at 2500 m.

SEIFRIZ—SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA. V. PLANT LIFE OF THE TRANSILIAN MOUNTAIN RANGE IN SEMIRECHJE, EASTERN TURKESTAN

Aster sedifolius in full flower, the umbelliferous *Libanotis montana*; and a *Draba*, possibly *D. incana*. *Sedum ewersii* occurs in great profusion, and still one flower remains of the well-named *Dianthus superbus*. Growing deep in the crevices of rocky mounds are two little inhabitants equally typical of alpine regions, *Silene supina* and *Asplenium septentrionale*.

The journey back to Almati is across the steppe as before. From Almati the trip up the Small Almatinka River can be taken; a day suffices, but two or three are better if one wishes to reach the high summits. The country is exquisite.

Fourteen kilometres south, toward the mountains, from Almati, on the Small Almatinka River, is Medeu (2200 m.) consisting only of a Government rest house (marked by a small circle in Fig. 2). The gorge starts here and leads to the glacier. The first foothill on the left bank at Medeu is a small knoll rising about 100 m. above the river. It is covered with *Picea* forests to the summit (2300 m.). Three peaks follow this knoll in succession up the left side of the gorge, each higher than the other, with correspondingly less forest and more meadow at the top. The next to the last peak (* in Fig. 2) is the highest alpine meadow of the chain (3000 m.). The last peak in the chain is a rocky crest, devoid of vegetation, and rising to an altitude of over 3200 m. It joins the main range not far from the snow-capped Almatinka Mountain (4267 m., marked with an oval in Fig. 2) which majestically heads the gorge and whose northern glacier gives rise to the Small Almatinka River.

The dominating tree of the Small Almatinka Valley is *Picea schrenkiana*. This spruce forms superb pure stands (Pl. XV, Phots. 4, 5, 6) throughout the higher mountains. It is at its best on the north slopes, the south slopes being usually devoid of a single specimen (Pls. XV, XVI, Phots. 7, 8). Even on the low foot hills, at Medeu, the spruce shows a marked north and south distribution. *Picea schrenkiana* does not attain the size of the Caucasian *Picea orientalis*, but it possesses a symmetry in form and regularity in distribution which is most striking (Pl. XV, Phot. 5).

Populus tremula and *Betula songorica (tianschanica)* form small woods on the lower slopes, never reaching as high as the spruce.

Both the left and right sides of the gorge are terminated by massive rocky peaks which join the Almatinka Mountain (Pl. XVI, Phot. 9). The last peak on the left (west) bank is preceded by a slightly lower mountain (* in Fig. 2), whose top is a grassy meadow (3000 m.). The mountain may readily be ascended, though the slope is steep. One first passes through a *Picea* forest and emerges now and then into scattered, open, subalpine pastures. The plant which, in autumn, predominates in these subalpine forest meadows is an *Alchemilla*. It occurs in such profusion that it appears to constitute the entire plant life of the meadows. There is considerable hesitation among Russian taxonomists to name an *Alchemilla* even when all the evidence is in. Without flowers, nothing definite can be said.

Aster altaicus, Geranium collinum, the endemic *Gentiana kirilowi (G. tian-schanica), Draba incana, Erysimum hieracifolium* and a *Potentilla* are still to be found in flower here at this season of the year.

Before the last *Picea* is passed between 2600 and 2800 m. fine large patches, fully 15 ft. in diameter, of the endemic *Juniperus pseudosabina (turkestanica)* are encountered. This prostrate juniper is scattered over the grassy mountain slopes in characteristic mammoth cushions of great number (Pl. XVI, Phot. 8).

The alpine meadow at the summit (Pl. XVI, Phot. 8) is covered with the grass *Festuca*. Less abundant, yet occurring in considerable quantity, is the small silver-leaved *Artemisia sericea*. Its presence here emphasizes the extraordinarily marked altitudinal distribution of this genus. If we recapitulate the species of this genus which we have encountered, there is *A. terrae albae*, of the steppes (800 m.), *A. absinthium* in the lower mountain valleys (1200 m.), *A. annua*, higher at the Lake (2400 m.), and *A. sericea* in the alpine pastures of the highest unglaciated Almatinka Mountains (3000 m.).

A single specimen of the delicate flower of *Alsine juniperina* remained in the alpine meadow here on September 26th.

From the summit of this mountain at an altitude of 3000 m. one obtains an excellent view of the surrounding country. The Transilian desert-steppe lies to the north (Pl. XVI, Phot. 8). From the canyon immediately below *Picea* forests climb to 2800 m. (Pl. XVI, Phot. 9) or even a little higher (Pl. XVI, Phot. 8). To the south, at the head of the Small Almatinka River, rests Mount Almatinka whose iced-capped peak rises to 4267 m. (Pl. XVI, Phot. 9).

DEPARTMENT OF BOTANY,
UNIVERSITY OF PENNSYLVANIA,
PHILADELPHIA, PA.

Phot. 8. Mammoth cushions of *Juniperus turkestanica* at
3000 m., with *Artemisia sericea* and *Festuca*.
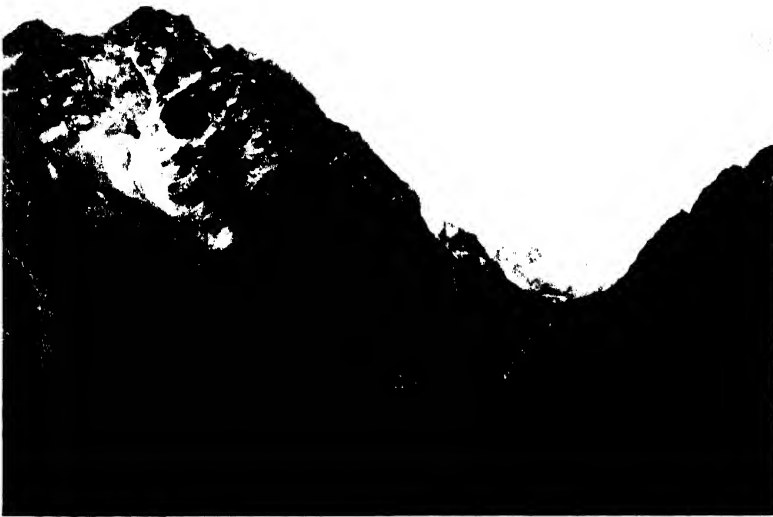
Phot. 9. Mount Almatinka (centre background) at the head of the Small Almatinka
River. The high rocky peak on the left is marked with a square in Fig. 2.

SEIFRIZ—SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF
SOVIET RUSSIA. V. PLANT LIFE OF THE TRANSILIAN MOUNTAIN RANGE IN
SEMIRECHJE, EASTERN TURKESTAN

ÜBER DEN WASSERHAUSHALT DER HOLZPFLANZEN

Von B. STEFANOFF und J. STOIČKOFF.

(*Department of Agriculture and Forestry, The University of Sofia.*)

UNTER allen Fragen, mit denen sich die experimentelle Ökologie befasst, ist die des Wasserhaushalts der Pflanzen eine der wichtigsten; ist doch das Wasser eine der Bedingungen, die das Äussere der Pflanzen und ihre geographische Verbreitung sowie die charackteristischen biologischen Eigenschaften der Pflanzendecke massgebend beeinflussen.

Jede Pflanze muss die Wassermenge, die sie abgiebt, derjenigen anzugleichen suchen, die sie aufnimmt. Diese Menge ist je nach der Organisation der Pflanzen verschieden. Die Experimentalökologie sucht einmal alle die äusseren Bedingungen zu erforschen, die in ihrer Gesamtheit den Vorgang der Wasseraufnahme und -abgabe bestimmen. Sie ist ferner bestrebt, die Beziehungen zu erklären, die zwischen der Wasseraufnahme und -abgabe und dem Bau der Wurzeln (des Absorptionssystems) und Blätter (des Transpirationssystems) und der die Wurzeln und Blätter verbindenden Gefässe (des Leitungssystems) bestehen. Die Ökologen haben die Beziehungen zwischen den Aussenbedingungen und dem Absorptions- und Transpirationssystem eingehend zu erforschen gesucht, der Bedeutung des Leitungssystems dagegen nur geringe Beachtung geschenkt. Nur Vesque, Eberhard, Joltkewitsch, Lebediniev und andere haben für eine ganze Reihe von Pflanzen Beziehungen zwischen den Aussenzuständen und dem Bau und der Wirkungsweise des Leitungssystems festgestellt. Die Versuche von Vesque und Eberhard[1] haben gezeigt, dass solche Pflanzen, die in trockener Luft oder unter anderen Umständen, die die Wasserabgabe fördern, wachsen, in Stamm und Blättern ein besser entwickeltes Leitungssystem besitzen.

In allerletzter Zeit hat dies Lebediniev bestätigt[2]. Joltkewitsch hat gefunden, dass die Luzerne der Dürre besser widersteht als der Klee und auch ein erheblich besser ausgebildetes Leitungssystem hat[3]. Besonders wertvolle Forschungen, die die Wirkung des Leitungssystems und seine Bedeutung für die Ökologie indirekt zum Ziele haben, stammen namentlich von Farmer, Huber, Ewart, Holmes u.a. und sind jüngsten Datums.

[1] J. VESQUE et CH. VIET, "De l'influence du milieu sur la structure anatomique des végétaux," *Ann. Sc. nat. Bot.* sér. VI, **12**, 1881, 167–176; P. H. EBERHARD, "Influence de l'air sec et de l'air humide sur la forme et la structure des végétaux," *Ann. Sc. nat. Bot.* sér. VII, **18**, 1903, 65–152.

[2] E. LEBEDINIEV, "Physiologische und anatomische Besonderheiten der in trockener und in feuchter Luft gezogenen Pflanzen," *Ber. d. d. bot. Ges.* **45**, 1927, 90.

[3] V. JOLTKEWITSCH, "On the question of the causes of varying drought resistance of clover and lucerne," *Journ. Exp. Agronomy,* **14**, 1913, 106. In Russian.

Farmer[1] verglich die Leitfähigkeit der Gefässe verschiedener Holzpflanzen. Er kam zu dem Schluss, dass die Gefässe immergrüner Sklerophyller eng sind und ihre Leitfähigkeit deshalb verhältnismässig niedrig ist und in engen Grenzen schwankt. Bei sommergrünen breitblättrigen Holzgewächsen fand er dagegen die Leitfähigkeit in der Regel verhältnismässig hoch und oft beträchtlich schwankend. Er schloss hieraus mit Recht, dass für die Beziehungen zwischen den Holzgewächsen und ihrem Standorte (besonders den Feuchtigkeitsverhältnissen) auch das Leitungssystem von grosser Bedeutung ist.

Zuletzt vergleicht Farmer die Leitungsfähigkeit des Holzes mit der Intensität des Wachstums desselben und sagt, dass die langsam wachsenden Holzarten sich fast immer durch ein Leitungssystem auszeichnen, welches das Wasser verhältnismässig langsam durch den Stamm führt. Diese ausserordentlich wichtigen Untersuchungsresultate Farmers sind später im Bezug auf eine ganze Reihe von südafrikanischen Holzarten von Bews[2] bestätigt worden. Bews selbst hat gefunden, dass die im Bau verhältnismässig primitiven immergrünen tropischen und subtropischen Formen sich in der Regel durch eine solche Holzstruktur auszeichnen, welche das Wasser mit einer nur ungenügenden Intensität emporführt. Derselbe Forscher ist auch der Ansicht, dass die Verbesserung des Leitungssystems der Dicotyledonen in Bezug auf ihre Leitungsfähigkeit in einem langsamen Entwicklungsprozess zu suchen ist. Den Schlussfolgerungen Farmers schliesst sich auch Huber an, der in einer ganzen Reihe von darauf bezughabenden Arbeiten die Untersuchungen über die Wasseraufnahme des Holzes erweitert und vervollkommt hat[3].

Wenn man davon ausgeht, dass die immergrünen Nadel- und Laubhölzer meist schwächer transpirieren als die sommergrünen und in Betracht zieht, dass nach Farmer u.a. die Gefässe der immergrünen eine geringere Leitfähigkeit haben als die sommergrünen, dann sollte man annehmen, die mit wenig Wasser sich begnügenden immergrünen könnten auch Wassermangel besser vertragen als die sommergrünen.

Dem widerspricht aber die Erfahrung, dass in Gegenden mit kontinentalem Klima jene Holzgewächse gegen Dürre am empfindlichsten sind, die am wenigsten Wasser abgeben, also auch die geringste Wassermenge brauchen. Daraus folgt, dass bei diesen in der Dürrezeit die Gefässe nicht einmal imstande sind, die verhältnismässig geringen Wassermengen zu leiten, die zum Ersatz des abgegebenen Wassers nötig sind.

---

[1] J. B. FARMER, "On the quantitative differences in the water conductivity of the wood in trees and shrubs," *Proc. Roy. Soc.* B, **90**, No. 628, pp. 218–250.

[2] J. W. BEWS, "Studies in the ecological evolution of the Angiosperms," *New Phytologist*, **26**, No. 1, 1927, 16.

[3] B. HUBER, "Beiträge zur Kenntnis der Wasserbewegung in der Pflanze," *Ber. d. d. bot. Ges.* **42**, 1924, 27; DERS., "Die Beurteilung des Wasserhaushaltes der Pflanze," *Jahrb. f. wiss. Bot.* **64**, 1925, Heft 5, S. 51–116; DERS., "Die physiologische Leitungsfähigkeit des Wasserleitungssystems der Pflanze," *Ber. d. d. bot. Ges.* **43**, 1925, 410; DERS., "Weitere quantitative Untersuchungen über das Wasserleitungssystem der Pflanzen," *Jahrb. f. wiss. Bot.* **67**, 1928, 877 ff.

Unsere eigenen Versuche bezweckten, die Höhe des Defizits im Wasserhaushalt verschiedener Holzgewächse während der Trockenzeit festzustellen.

Gegenden, deren Klima die Pflanzen längere oder kürzere Zeit der ungünstigen Wirkung der Dürre aussetzt, eignen sich besonders gut für Versuche, die die grosse Bedeutung des Leitungssystems für die geographische Verbreitung der Holzpflanzen ermitteln sollen. Solche Gegenden bietet Ost-, besonders aber Südosteuropa mit einem auf weite Flächen kontinentalen Klima. Zieht man dort in Parken und Baumschulen verschiedene Holzpflanzen teils heimischer teils fremder Herkunft im gleichen Entwicklungszustande, so findet man in ihrem Verhalten gegen die Dürre und in ihrer Weiterentwicklung die beträchtlichsten Unterschiede.

Dies verschiedene Verhalten hat eine ganze Reihe von Gründen. Der Hauptgrund ist wohl die spezifische Konstitution des Protoplasmas der verschiedenen Holzgewächse. Man kann aber vielfach beobachten, dass auch diejenigen Organe und Gewebe von grosser Bedeutung sind, welche Aufnahme, Transport und Abgabe des Wassers besorgen. Man muss daher wie auch Stocker[1] betont, zur Klärung der Frage der geographischen Verbreitung der Holzpflanzen und des Verhaltens von kultivierten Holzpflanzen unter einem ganz bestimmten Klima ihren Wasserhaushalt und die Mittel zur Herstellung seines Gleichgewichts in Betracht ziehen.

Ohne Versuche lässt sich die Bedeutung des einen Systems nicht gegen die des andern abgrenzen. Aber es ist augenscheinlich, dass die Leitfähigkeit des Gefässystems einer bestimmten Holzpflanze sehr wichtig ist für ihr Verhalten gegenüber dem kontinentalen Klima, also für ihre Fähigkeit, die Dürre mit oder ohne Schaden zu überstehen. Unsere Versuche zielen darauf hin, die grosse Bedeutung hervorzuheben, die dem Leitungssystem neben dem Absorptions- und Transpirationssystem für die Pflanzengeographie zukommt. Zugleich wollten wir die Ergebnisse nachprüfen, die Farmer, Huber u.a. beim indirekten Studium der Leitfähigkeit der Gefässe gefunden haben. Unsere Versuche bestätigen, wenn auch an Zahl ungenügend, den oben gezogenen allgemeinen Schluss. Als Aufgabe hatten wir uns gestellt, zu ermitteln, wie der Wasserhaushalt während der Vegetationsperiode unter der Einwirkung wechselnder Aussenbedingungen schwankt. Wir nahmen an, diese Schwankungen ergäben sich einfach durch Messung der in der gleichen Zeit aufgenommenen und abgegebenen Wassermengen. Überwiegt die Transpiration die Absorption, so entsteht, wie Montfort das ausdrückt, eine Unterbilanz im Wasserhaushalt. In diesem Falle können die Gefässe nicht soviel Wasser zuleiten wie abgegeben wird. Je grösser die Unterbilanz bei einer bestimmten Holzpflanze ist, um so weniger ist diese den Aussenbedingungen angepasst. Unter natürlichen Verhältnissen könnte eine Unterbilanz durch zu geringe Absorptionsmöglichkeit verursacht werden, und diese wieder hängt

[1] O. Stocker, "Ueber die Höhe des Wasserdefizits bei Pflanzen verschiedner Standorte," *Erdészeti Kiesérletek*, **31**, 1929, 114.

von Bau und Form der Wurzeln und von der Menge und Verteilung des Wassers im Boden ab. Um diesen Faktor auszuschalten, haben wir bei unseren Versuchen abgeschnittene in Wasser gestellte Zweige verwendet. Wir nahmen an, dass wir dadurch für die Wasserabsorption aller geprüften Pflanzenarten ziemlich gleiche Bedingungen schafften und schlossen weiter, dass die Unterbilanz im Wasserhaushalte darum nur eine Folge der zu geringen Leitfähigkeit der Gefässe sein könne.

Das Hauptgewicht legten wir darauf, den Einfluss des Sättigungsdefizits der Luft auf die Schwankungen im Wasserhaushalte zu ermitteln. Denn dies Defizit bedingt, wie man heute allgemein annimmt, geradezu den Transpirationsverlauf[1]. Bei unserer Versuchsanordnung war eine Temperaturerhöhung fast immer von einer Erhöhung dieses Defizits, ein Sinken der Temperatur von einem Sinken des Defizits begleitet. So setzten wir das Schwanken des Wasserverbrauchs mit dem des Sättigungsdefizits und der Temperatur in ständige Wechselbeziehung.

Der wesentlichste Teil unserer Versuche bestand, wie schon erwähnt, in der einfachen Messung des Wasserverbrauchs der unter Wasser abgeschnittenen Zweige, die wir dann der freien Transpiration aussetzten. Dazu haben wir das gewöhnliche, auch sonst für solche oder andere Zwecke gebrauchte Potometer von Pfeffer benutzt[2]. Wir haben periodisch den Wasserverbrauch verschiedener etwa gleich grosser Zweige derselben Holzpflanzenart gemessen, weil uns die Bedingungen fehlten, an ein und demselben Zweige das Schwanken des Wasserverbrauchs im Vergleich mit dem Schwanken des Sättigungsdefizits und der Temperatur zu bestimmen. Wir trafen alle Vorsichtsmassnahmen, die bei Versuchen mit Hilfe des Potometers üblich sind, und liessen dann die Zweige 4 Stunden lang frei transpirieren, und zwar von 10 Uhr vormittags bis 2 Uhr nachmittags, also gerade in der Zeit, wo die Transpiration ihre grösste Höhe erreicht[3], infolge dessen auch der Wasserverbrauch sein Maximum erreichen musste.

Die Menge des verdunsteten Wassers ermittelten wir durch Wägen. Die Menge des von den Zweigen aufgenommenen Wassers setzten wir gleich dem Verlust, den die Potometerbürette anzeigte. Wir arbeiteten mit runden Zahlen. Das machte die übliche Korrektur der Messungen und Ergebnisse überflüssig. So konnten wir fast während einer ganzen Vegetationsperiode eine ziemlich grosse Anzahl Versuche mit einer ganzen Reihe von Holzpflanzen machen. Wir achteten darauf, dass jede geprüfte Art verschiedenen Tem-

---

[1] O. STOCKER, "Die Transpiration- und Wasserökologie nordwestdeutscher Heide- und Moorpflanzen," *Zeitschr. f. Botanik*, **15**, 1–40; D. SZYMKIEWICZ, "Sur l'importance du déficit hygrométrique pour la phytogéographie écologique," *Acta Soc. bot. pol.* **1**, 1924, No. 1, p. 12.

[2] Vergl. A. BURGERSTEIN, *Die Transpiration der Pflanze*, Jena, 1920, II. Teil, S. 31; Н. Максимов Физиологические основы засухо устойчивсти растений Ленинград 1926 стр 121.

[3] Vergl. L. J. BRIGGS and H. J. SCHANTZ, "Hourly transpiration rate on clear days as determined by cyclic environmental factors," *Journ. Agr. Res.* **9**, 1916, 227–292.

peraturen und Sättigungsdefiziten ausgesetzt wurde. Schliesslich haben wir, um etwaige Versuchsfehler zu vermeiden, auch dafür gesorgt, dass ein stärkeres oder schwächeres Austrocknen der vegetativen Organe während des Versuches unterblieb. Zu diesem Zwecke wurden die Zweige einige Stunden, bisweilen sogar bis zu 24 Stunden, völlig in Wasser getaucht.

In den Tabellen (S. 100-104) bringen wir die Ergebnisse unserer Versuche. Die Holzgewächse folgen einander in dieser Reihe: (I) Nadelhölzer; (II) Immergrüne Laubhölzer; (III) Sommergrüne Laubhölzer mit stark schwankendem Wasserverbrauch, während der Trockenzeit auch mit erheblicher Unterbilanz; (IV) Sommergrüne Laubhölzer mit schwach schwankendem Wasserverbrauch und mit unerheblicher Unterbilanz während der Trockenzeit. Die erste Spalte der Tabelle enthält den Tag des Versuchs, die 2. die Temperatur in ° C., die 3. das Sättigungsdefizit, die 4. die Länge des Zweiges in cm., die 5. sein Gewicht in gr., die 6. die Menge des absorbierten Wassers in gr., die 7. die Menge des transpirierten Wassers in gr., die 8. die Unterbilanz in gr., wenn eine solche vorhanden ist, die 9. die Unterbilanz in %.

Korrektur der erhaltenen Ergebnisse.

Zunächst wollen wir das bei den Versuchen angewandte Verfahren kritisieren und die Genauigkeit der Ergebnisse nachprüfen. Hierbei sind zuerst zwei Fragen zu beantworten: (1) Können wir wirklich in dieser Art das natürliche Mass der Transpiration und der Leitfähigkeit bestimmen? Verlaufen also diese zwei Vorgänge in abgeschnittenen Zweigen ebenso wie unter natürlichen Verhältnissen? (2) Lassen sich die Ergebnisse der Versuche mit den verschiedenen Holzpflanzenarten mit einander vergleichen, wenn wir die verschiedene Grösse und das verschiedene Gewicht der einzelnen Zweige oder den Unterschied in der Grösse ihrer Transpirationsfläche und der Grösse und Länge ihrer Leitungsfläche ins Auge fassen?

Im voraus muss man sich darüber klar sein, dass die Grössen, die wir für die Wasserabgabe und für die Wasserleitung erhalten haben, bei weitem nicht der Wirklichkeit entsprechen. Fürs erste haben wir den Wurzeldruck hierbei überhaupt nicht beachtet[1]. Weiter ist sicher durch das Abschneiden der Zweige sowohl die Transpiration wie die Leitung des Wassers durch die Gefässe ziemlich gestört worden, so dass beide Vorgänge anders verlaufen als unter natürlichen Verhältnissen. Man hat hier zuerst an die Veränderung der Kohäsionskraft der Wasserteilchen in den Gefässen zu denken, die, wie man später sehen wird, für die Stärke der Transpiration nicht ohne Bedeutung ist. Haben doch Gates, Muenscher, Burgerstein, Renner u.a. durch viele Versuche gezeigt, dass das Abschneiden eines Zweiges Verlauf und Stärke

---

[1] In diesem Falle haben wir vor Augen gehabt die in letzter Zeit geäusserte Behauptung, dass der Wurzeldruck keinen Einfluss auf das Hinaufsteigen des Wassers in den Leitungsgefässen ausübt. (Vergl. A. A. Ivanov, "Sur la distribution et le rôle de la pression dans les racines," *Mélanges botaniques offerts à M. Borodine à l'occasion de son jubilé,* 1927.)

seiner Transpiration ändert[1]. Dasselbe gilt von der Aufsaugung des Wassers, die durch das Abschneiden für kurze Zeit ziemlich herabgesetzt wird[2]. Unsere Versuche erstreben aber nur relative Werte. Wir glauben, dass man eine Vorstellung der relativen Grösse von Transpiration und Leitfähigkeit bei den verschiedenen Holzpflanzen erhalten kann, wenn man abgeschnittene Zweige gleichen Bedingungen aussetzt, mögen auch beide Vorgänge dabei nicht ihren natürlichen Verlauf nehmen. Verwendete man zur Feststellung des Wasserverbrauchs einer Holzpflanze bei verschiedenem Sättigungsdefizit Zweige verschiedenen Ausmasses, also mit verschiedener Grösse der Transpirationsfläche und der Leitungsstrecke, so würden sicher die Fehler recht gross sein. Ganz genaue Ergebnisse könnte man nur dann erhalten, wenn man stets mit ein und demselben Zweige arbeitete. Das wäre aber nur unter schwer erfüllbaren Bedingungen möglich.

Bei unseren Bedingungen, d.h. bei der Auswahl von nach Art und Dimension annähernd gleichen Zweigen, kommt man in die Lage Grössen zu vergleichen, die nach ihrem Wesen untereinander nicht vergleichbar sind. Man muss sich aber vor Augen halten, dass unseres Erachtens die genannten Fehler auch dann nicht zu vermeiden wären, wenn man den Versuch unternehmen würde, die einzelnen Daten zu konstanten Grössen zu reduzieren, wie z.B. zu Gewichtseinheiten, zu der Einheit der Transpirationsfläche oder zu jener der Leitfläche. Bei allen Versuchen ähnlicher Art müssen wir stets die möglichen Schwankungen individuellen Charakters vor Augen haben, die meistens sehr bedeutend sein können. So z.B. ersieht man aus den von Farmer erhaltenen Resultaten, dass die Grösse der Leitungskapazität in den Zweigen einer und derselben Art stark wechselt und von dem Alter und dem Stammsystem des Baumes, sowie noch von einer ganzen Reihe individueller Ursachen abhängig ist. Jaccard und Rübel haben auch festgestellt, dass die Proportionalität zwischen der Transpiration und der Leitfläche in einer und derselben Holzpflanze ausserordentlich stark variiert, was nach ihrer Meinung der an verschiedenen Stellen des Baumes ungleichen Leitungsfähigkeit des Holzes zuzuschreiben wäre[3]. Wahrscheinlich lässt sich dasselbe auch von der Intensität der Transpiration sagen, die ebenfalls grosse individuelle Schwankungen zeigen wird, die von manchen zufälligen Besonderheiten des Blattsystems, von dem Alter der Blätter, ja sogar von dem Alter der Zweige, auf denen sich diese Blätter entwickelt haben, abhängig sind. Da wir uns daher vollständig klar waren, dass ein jeder Versuch eine grössere Präzision bei solchem Experimentieren anzustreben an den soeben erwähnten Schwierigkeiten gescheitert sein wurde haben wir

---

[1] Vergl. A. Burgerstein, *loc. cit.* S. 31–33; und B. Huber, "Zur Methodik der Transpirationsbestimmung am Standort," *Ber. d. d. bot. Ges.* **45**, 1927, 611.

[2] F. Darwin and R. W. Phillips, "On the transpiration stream in cut branches," *Proc. Camb. Phil. Soc.* **5**, 1886.

[3] B. Huber, "Die Beurteilung der Wasserhaushaltes der Pflanze," *Jahrb. f. wiss. Bot.* **64**, 1925, Heft 5, S. 93; Ders, "Weitere quantitative Untersuchungen über das Wasserleitungssystem der Pflanze," *Jahrb. f. wiss. Bot.* **67**, 1928, 916.

angenommen, dass wenigstens das Ausmass der Wasserbilanz für gewisse Variationen in den Dimensionen der von uns benutzten Zweigen—soweit die Beziehungen zwischen der Transpirationsfläche und der Leitmasse in Betracht kommen—ein und dasselbe bleibt oder in sehr unbedeutenden Grenzen schwankt. Auf diese Art, sogar wenn wir uns vor Augen halten, dass bei einer progressiven Vergrösserung der Länge der Leitungsgefässe, etwa von 10–20 und sogar 50 cm., die Widerstandskraft bei der Durchleitung des Wassers proportional wächst, kann der Unterschied in dem sich vergrössernden Widerstand nicht so gross angenommen werden, dass er eine physiologische Gleichstellung von Zweigen mit den genannten Dimensions-Variationen absolut unmöglich machen. Dasselbe kann auch von dem Verhältnis zwischen der Transpirationsfläche und der Leitmasse gesagt werden. Die Schwankungen in den Dimensionen der Zweige können nicht so gross sein, dass sie eine Vergleichung der erhaltenen Resultate unmöglich machen. In allen Fällen sind die grösseren Schwankungen eher Abweichungen, die von den individuellen Eigenschaften und nicht von den Unterschieden in der Länge der Zweige abhängen, zuzuschreiben.

Einige unserer Versuche deuten auf den Einfluss verschiedener Zweiggrösse auf den Wasserverbrauch hin. Verschieden grosse Zweige von *Abies alba*, *Acer pseudoplatanus* und *Quercus rubra* wurden gleichzeitig geprüft (siehe die Tabellen). In allen drei Fällen haben wir gefunden, dass geringe Schwankungen in der Länge und dem Gewicht der Zweige, also in der Grösse der Transpirationsfläche und der Leitungsstrecke zu keinen erheblichen Schwankungen im Wasserverbrauch führen.

Alle Fehler dieser Art können durch eine grosse Zahl Versuche auf ein ganz geringes Mass beschränkt werden.

Allgemeine Schlüsse über den Wasserverbrauch der Holzpflanzen auf Grund der bisherigen Forschungen.

An erster Stelle ist hervorzuheben, dass die Zahl, die die Wechselbeziehungen zwischen der durch Transpiration abgegebenen und der von den Holzgefässen geleiteten Wassermenge ausdrückt, je nach den Aussenbedingungen erheblich schwankt. Ferner ist diese Zahl je nach der Art der Holzgewächse bei gleichen Lebensbedingungen sehr verschieden. Am stärksten hängen diese Schwankungen von jenen Aussenbedingungen ab, welche den Transpirationsverlauf bestimmen. Wie wir schon erwähnt haben, steht das Sättigungsdefizit unter diesen Bedingungen an erster Stelle. Die Erhöhung dieses Defizits hat immer die Verstärkung der Transpiration zur Folge. Aber bei einer ganzen Reihe von Holzpflanzen ruft die starke Transpiration während mancher Tagesstunden und Jahreszeiten zugleichzeitig eine langdauernde Austrocknung der vegetativen Organe hervor, die bei den einzelnen Arten sehr verschieden ist, je nach ihrer Fähigkeit, das durch die Transpiration verlorene Wasser zu ersetzen. Wir haben die Austrocknung, welche der Grösse der

Unterbilanz entspricht, zu der Zeit gemessen, wo die Transpiration am stärksten war. Ein Wasserdefizit, das infolge der während des Tages erhöhten Transpiration entstanden ist, wird durch Aufhören der Transpiration in der Nacht völlig beseitigt, wie auch Maximov bemerkt hat[1]. In diesem Falle hätten wir also bei den günstigsten Aussenbedingungen statt einer lang andauernden nur eine vorübergehende Austrocknung der vegetativen Organe während der Tagesstunden. In Gegenden mit trockenem Klima kann indessen der durch die starke Verdunstung während der Tagesstunden zu gering gewordene Wassergehalt nicht immer in der folgenden Nacht vollständig wieder hergestellt werden[2]. Das trifft für solche Gegenden und Länder zu, in denen, wie in Bulgarien, eine lang andauernde Sommerdürre eine gewöhnliche, fast jedes Jahr wiederkehrende Erscheinung ist. So kann eine starke Austrocknung oder ein lang andauernder Wassermangel der vegetativen Organe eintreten, der die Entwicklung der Bäume ungünstig beeinflusst. Die ungünstige Wirkung dieses Austrocknens tritt in den Parken und Baumschulen Sofias bei einer Reihe von Nadelhölzern und sommergrünen Bäumen und Sträuchern in verschiedener Weise zu Tage.

Das ungleiche Verhalten der verschiedenen Holzpflanzen der ungünstigen Wirkung der Trockenheit gegenüber zeigt sich äusserlich darin, dass sie eine nach der andern verschwinden, je kontinentaler das Klima wird. Infolge dessen kann von den Holzarten, die man in den durch feuchteres Klima ausgezeichneten Teilen des Kontinents antrifft, nur eine geringe Anzahl in das Kontinentinnere eindringen.

So fehlen im Innern des Kontinents ohne Ausnahme alle immergrünen Bäume und Sträucher, die nach Höhnels Forschungen schwächer transpirieren als die sommergrünen Arten[3]. Die Ursachen dieses schwächeren Transpirierens sind bis jetzt ungenügend erkannt. Ausser an die geringere Grösse der Saugfläche, die nach Höhnel bei Nadelbäumen nur etwa $\frac{1}{6}$ so gross ist wie bei Laubhölzern, muss man in erster Reihe an die schwächere Entwicklung des Wasserleitungssystems und der Transpirationsorgane und an das homogene Holzgewebe denken, das aus Tracheïden und englumigen Gefässen besteht. Wenn man die Annahme Hubers[4], die Kohäsion der Wasserteilchen vergrössere sich mit der Abnahme der Gefässweite, als sehr wahrscheinlich ansieht, wird man auch die geringere Leitfähigkeit dieses homogenen Holzgewebes annehmen müssen. Auch Renner hat nachgewiesen, dass die Stärke der Transpiration sehr von der Stärke der Kohäsion der Wasserteilchen in den Gefässen abhängt. So kommt man zu dem Schluss, dass die schwache

---

[1] A. N. Maximov, *The Plant in Relation to Water*, English edition, London, 1929, p. 151.

[2] W. S. Iljin, "Der Einfluss des Wassermangels auf die Kohlenstoff-Assimilation," *Flora*, **116**, 1923, 360.

[3] Fr. Höhnel, "Weitere Untersuchungen über die Transpirationsgrösse der förstlichen Hölzgewächse," *Mitteil. aus dem Forstversuchswesen Österreichs*, **2**, 1880.

[4] B. Huber, "Die physiologische Leitungsfähigkeit des Wasserleitungssystems der Pflanze," *Ber. d. d. bot. Ges.* **43**, 1925, 417.

Transpiration wie bei den Nadelbäumen so auch bei mehreren immergrünen Sklerophyllen ebenso wie ihr Xeromorphismus eine ursprüngliche Erscheinung ist, die vom primitiven Bau der Leitgefässe selbst abhängt[1]. Es beruht also die schwache Transpiration und die schwächere Leitfähigkeit auf ein und derselben Struktureigenschaft. Die höhere Entwicklung des Leitungssystems, d.h. die Verbesserung und Verstärkung seiner Leitfähigkeit, wird auch von einer Verstärkung der Transpiration begleitet.

Hiernach stehen die immergrünen Sklerophyllen in vollem Gegensatz zu jenen Holzpflanzen, die das bestentwickelte Leitungssystem haben. Die gute Entwicklung eines Leitungssystems werden wir vor allem an langen weiten Gefässen erkennen. An erster Stelle stehen hier die Arten von Eichen und Rüstern mit ringporigem Holzgewebe. Nach den Ergebnissen unserer Versuche sind dazu auch eine ganze Reihe von Bäumen zu rechnen, die ein zerstreutporiges Holzgewebe haben und während der Trockenzeit keine erhebliche Unterbilanz zeigen. Das sind nach unseren Ergebnissen die Erle, die Weissbuche, die Rotbuche, der Spitzahorn, die Silberlinde, die Silberpappel und *Acer dasycarpum*. Es wurde oben schon erwähnt, dass auch die Transpirationsstärke mit der Erhöhung der Unterbilanz, d.h. der Erhöhung der Leitfähigkeit der Holzgefässe, wächst. So kommen wir zu dem Schluss, der als eine fast allgemeine Regel gilt: *Je besser eine Holzpflanze durch Verstärkung ihrer Leitfähigkeit den ungünstigen Einflüssen der Trockenheit angepasst ist, um so stärker ist unter sonst gleichen Bedingungen ihre Transpiration.* Als Beispiel kann die Eiche dienen, die am tiefsten in den Kontinent eindringt und von allen europäischen Holzpflanzen am besten die ungünstige Wirkung der Trockenheit aushält. Man erinnere sich an die eben erwähnte Regel, dass eine Pflanzenart um so besser an die Trockenheit angepasst ist, je besser ihr Leitungssystem entwickelt ist. Dass die Stärke der Transpiration mit der Zunahme der Trockenheit steigt, kommt uns widersinnig vor, ist aber doch eine von vielen Forschern festgestellte Tatsache. Anders ausgedrückt: Diejenigen Holzpflanzen sind dem Trockenklima am besten angepasst, die sich bei gleichen äusseren Bedingungen durch höchste Stärke der Transpiration auszeichnen.

In einigen Fällen aber ergeben Versuche Widersprüche zu diesen allgemeinen Schlussfolgerungen. So zeigen z.B. Linde, Weiss- und besonders Rotbuche bei stärkster Temperaturerhöhung und grösstem Sättigungsdefizit keine erhebliche Unterbilanz und doch wissen wir dass sie, die das Klima der Ebene von Sofia schlecht vertragen. Gerade das Gegenteil ist der Fall mit einer Gruppe von sommergrünen und sogar von immergrünen Arten (einschliesslich einiger Nadelhölzer). Diese Gruppe von Baumarten hat eine erhebliche Unterbilanz während der Trockenzeit und kann doch die ungünstigen Wirkungen des kontinentalen Klimas gut oder doch wenigstens aus-

---

[1] Für die Coniferen seit langem von M. C. Stopes vorausgesetzt ("The 'Xerophytic' Character of the Gymnospermae," *New Phytologist*, 6, 1907).

reichend ertragen. Dahin gehören z. B. von den Bäumen der 3. Gruppe
Gleditschia, Robinia pseudacacia, Morus alba, Juglans regia und von den
Nadelhölzern *Thuja orientalis*. Diese Ausnahmen zeigen uns, dass neben dem
Bau des Leitungssystems und seiner Leitfähigkeit für die Anpassung der
Holzpflanzen an die Trockenheit auch andere morphologische und physio-
logische Eigenschaften dieser Pflanzen von grosser Bedeutung sind. Wir
brauchen hier nur den Bau des Wurzelsystems und seine Stellung im Boden
zu nennen. Deshalb können vielleicht die flachwurzelnden Bäume, Linde,
Rotbuche, z.T. auch Weissbuche in Gegenden mit kontinentalem Klima nicht
gedeihen, weil dort die oberen Erdschichten lange Zeit trocken sind und den
Wurzeln das Grundwasser nicht oder schwer zugänglich ist. Schliesslich kann,
wie schon Maximov meint, eine innere Eigenschaft, ihre Dürreresistenz,
manche Arten befähigen, die Trockenheit lebend zu überstehen[1].

Das Leitungssystem ist einerseits der Regler der Wasserbilanz der Pflanzen,
tritt aber anderseits auch als wichtiger Faktor für den Wuchs der Holzge-
wächse auf. Es ist eine altbekannte Tatsache, dass die angepflanzten oder
wildwachsenden mitteleuropäischen Holzarten in den kontinentalen Gegenden
Europas fast niemals ihre volle Höhe erreichen. Das gilt auch für manche
immergrüne Arten, wie Eibe, Stechpalme, und Buchsbaum. Diese trifft man
nahe der Küste des atlantischen Ozeans als Bäume von bedeutender Höhe.
In Südosteuropa nehmen sie selbst unter günstigsten Bedingungen Strauch-
form an. Die Ursachen dieser Wuchsverkleinerung müssen einmal im Bau und
der Leitfähigkeit des Holzgewebes liegen, anderseits in den Eigenschaften des
Klimas, sodass eine Unterbilanz im Wasserhaushalt auftritt oder sich ver-
grössert, sei es durch Verstärkung der Transpiration, sei es durch Verlängerung
der Leitbahnen. Die einzige Möglichkeit den Transport der Wassermenge zu
erleichtern, die eine bestimmte Holzpflanze bei erhöhter Transpiration braucht,
liegt in der Verkürzung der Strecke zwischen dem absorbierenden Wurzel- und
dem transpirierenden Blattsystem. Die Holzpflanzen haben also in der
Verkürzung des Stammes und zugleich im Übergang von der Stamm- zur
Strauchform das letzte Kampfmittel gegen die Dürre. Mit andern Worten, die
Verkürzung der Wasserleitungsorgane, d.h. die Verkürzung des Stammes
selbst tritt als ein Selbstregler auf, der die Leitfähigkeit einer bestimmten
Holzpflanze in wirksame Wechselbeziehung zu ihrer Wasserabgabe bringt.

Eine Verkürzung des Stammes und Verwandlung der Baum- in die Strauch-
form erleiden hauptsächlich die Holzarten mit homogenem Holzgewebe und
engsten Leitungsgefässen. Solche Holzpflanzenarten können nur in extrem
feuchtem Klima erhebliche Höhe erreichen und zwar bei sehr geringem
Wasserverbrauch (z.B. die riesigen Koniferen im pazifischen Nordamerika wie
Sequoia, Abies grandis, Pseudotsuga Douglasii u.a. oder die immergrünen
Sklerophyllen in der feuchten Zone der Kanarischen Inseln).

---

[1] N. MAXIMOV, "Physiologisch-ökologische Untersuchungen über die Dürreresistenz der
Xerophyten," *Jahrb. f. wiss. Bot.* **62**, 1923, 139.

Hiernach ist die Strauchform als ein im allgemeinen sekundärer biologischer Typus anzusehen, bedingt durch die Beziehungen zwischen Bau und Länge des Leitungssystems auf der einen und den Eigenschaften des Klimas auf der andern Seite. Die Sträucher sind im allgemeinen auf dem Wege der durch das ungünstige Klima hervorgerufenen Verkürzung des Stammes entstanden, also des Leitungssystems, der Strecke zwischen Absorptions- und Transpirationsorganen.

Zum Schluss sei nochmals hervorgehoben, dass die Pflanzendecke der Erde in ihrer Entwicklung sich an die ungünstige Wirkung zunehmender Dürre angepasst hat, eine Entwicklung, die noch erkennbar ist in der Vervollkommnung des Leitungssystems und damit der Erleichterung des Wasserumlaufs. Nach diesem Gesichtspunkte kann man die aussertropischen Holzgewächse in nachfolgende Hauptgruppen einteilen, die durch eine ganze Reihe von Übergängen verbunden sind, welche gleichzeitig die einzelnen Stufen der Anpassung darstellen:

(1) Immergrüne Sklerophylle. Sie sind an das feuchte Klima mit seinen Extremen gebunden. Der Palaeomorphismus dieser nach Abstammung und Entwicklungsstufe primitiven Holzpflanzen zeigt sich im hohen Grade auch im Leitungssystem, das entweder nur aus Tracheïden (Gymnospermae) oder aus Tracheïden und engen offenen Gefässen besteht. Das Holzgewebe ist im allgemeinen dicht und homogen. Das Wachstum und die anderen physiologischen Funktionen verlaufen ununterbrochen, doch langsam. Das Gesagte gilt nicht nur für die Transpiration und die Wasserleitung, sondern auch für die Zuwachsvorgänge. Die immergrünen Sklerophyllen, oft unrichtig Xerophilen genannt, müssen in ihrer Gesamtheit als echte Xerophoben gelten, da ihre Verbreitung hauptsächlich an ein feuchtes Klima gebunden ist.

(2) Sommergrüne Mesophylle mit periodischen, jedoch intensiven Lebensvorgängen, die bei hoher aber stark schwankender Luftfeuchtigkeit und bei stets feuchtem Boden verlaufen. Ein entwickelterer Typ, der Arten umfasst mit einem Leitungssystem, das an starke Transpiration während der Aktivperiode angepasst ist. In den Blättern ist das Mesophyllgewebe stark entwickelt. Sie vertragen deshalb auch keine starke Austrocknung. Dieser Typus hat meist ein flaches Wurzelsystem und gedeiht am besten bei einem Klima mit häufigen und starken Sommerregen. Hierher gehören die gemischten Waldbestände der Ostküsten der Kontinente und der feuchten Gebirgsgürtel.

(3) Sommergrüne Xerophylle mit Periodizität der Lebensvorgänge, die bei nicht beständiger Luftfeuchtigkeit und oft bei andauernd trockenen Oberschichten des Bodens verlaufen. Sie gedeihen bei tiefliegendem Grundwasser und die meisten Arten haben ein tief eindringendes, vertikales, stark entwickeltes Wurzelsystem. Das Holzgewebe ist öfter ringporig und stark leitfähig und die Holzgefässe sind oft weit. Die Transpiration verläuft infolge der grossen Lufttrockenheit schnell und kräftig. Die Blätter haben ein

schwach entwickeltes Mesophyllgewebe, dagegen starkes mechanisches und gutes Leitungsgewebe. Sie können der Dürre gut widerstehen. Die Lebensvorgänge sind infolge der ungenügenden Wasserzufuhr verlangsamt. Es gehören hierher die Wälder in den innern Teilen der Kontinente, die aus wenigen Arten zusammengesetzt sind und anhaltende Dürre ohne Schaden vertragen. Ein Beispiel solcher Vegetation sind die reinen Eichenbestände Ost- und Südeuropas.

(4) Immergrüne Xerophyten. Die aktiven Lebensvorgänge (Zuwachs und Reproduktion) sind von sehr kurzer Dauer und periodisch oder aperiodisch. Es gehören hierher Holzpflanzen von sehr geringer Grösse, tief eindringendem Wurzelsystem, öfter zum Teil oder ganz verkümmerten oder verkleinerten Blättern und stark ausgeprägter Dürreresistenz. Eine ganze Reihe anderer Eigenschaften unterstützt den Pflanzenorganismus in seinem Kampfe gegen die anhaltende Dürre. Die Pflanzengruppe der Xerophyten stellt eine sehr verwickelte Gesamtheit von biologischen Typen dar, welche extreme Luft- und Bodentrockenheit vertragen und daher die Gegenden mit Wüsten- oder Halbwüstenklima bewohnen können. Die Wüstenpflanzen sind geschichtlich eine moderne Gruppe und das Endglied der Entwicklung der Pflanzendecke der Erde, die so verläuft, dass das Wasser als Lebensnotwendigkeit immer entbehrlicher wird.

I. Nadelhölzer.

1. *Picea excelsa.*

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Tag des Versuchs	Temperatur in ° C.	Sättigungsdefizit	Länge des Zweiges in cm.	Gewicht des Zweiges in gr.	Menge des absorbierten Wassers in gr.	Menge des transpirierten Wassers in gr.	Unterbilanz in gr.	Unterbilanz in %
16. iii. 29	4·2	2·23	—	187·5	8·4	5·0	—	0
17. iii. 29	7·6	3·86	—	146·0	10·0	5·0	—	0
18. iii. 29	4·2	2·18	64	149·0	6·2	3·0	—	0
10. vii. 29	21·2	9·28	70	165·5	7·8	8·0	0·2	2·50
25. vii. 29	26·2	14·61	65	247·0	8·6	8·0	—	0
21. viii. 29	25·7	11·98	76	160·0	19·7	20·7	1·0	5·00
14. ix. 29	24·0	11·44	65	214·5	42·2	46·2	4·0	8·80
30. ix. 29	14·4	5·13	80	243·5	28·9	31·8	2·3	7·37

2. *Sequoia gigantea.*

22. iii. 29	7·3	3·24	34·0	57·0	3·5	1·0	—	0
10. vi. 29	29·5	16·83	58·0	145·0	19·5	23·5	4·0	17·0
26. vi. 29	26·2	12·07	70·0	206·0	19·5	22·5	3·0	13·3
11. vii. 29	20·6	9·28	70·0	197·0	15·0	13·5	—	0
24. vii. 29	25·7	13·5	82·0	241·0	25·4	18·5	—	0
6. viii. 29	27·4	11·63	65·0	192·0	25·0	25·5	0·5	2·0
14. ix. 29	24·0	11·44	57·0	190·5	61·6	63·1	1·5	2·5
26. ix. 29	15·6	5·82	60·0	204·5	35·2	35·7	0·5	1·4

3. *Abies alba.*

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Tag des Versuchs	Temperatur in ° C.	Sättigungsdefizit	Länge des Zweiges in cm.	Gewicht des Zweiges in gr.	Menge des absorbierten Wassers in gr.	Menge des transpirierten Wassers in gr.	Unterbilanz in gr.	Unterbilanz in %
16. iii. 29	4·2	2·23	—	203·0	2·5	2·0	—	0
17. iii. 29	7·6	3·86	—	88·0	3·4	3·0	—	0
18. iii. 29	4·2	2·18	67	88·2	3·6	2·0	—	0
19. iii. 29	6·2	3·0	72	348·5	5·4	4·8	—	0
19. iii. 29	6·2	3·0	63	100·0	2·0	1·0	—	0
19. iii. 29	6·2	3·0	52	92·0	3·8	4·0	0·2	5·0
20. iii. 29	13·7	5·5	52	90·0	6·0	5·5	—	0
11. vi. 29	30·2	16·29	70	385·0	18·5	21·5	3·0	14·0
28. vi. 29	25·7	10·22	77	277·5	6·8	16·5	9·7	59·0
11. vii. 29	20·6	9·28	80	277·0	14·3	13·0	—	0
24. vii. 29	25·7	13·5	77	249·0	8·8	11·5	2·7	23·5
5. viii. 29	26·7	11·3	70	182·0	6·4	8·5	2·1	25·0
14. ix. 29	24·0	11·44	60	106·0	10·6	13·0	2·4	19·0
30. ix. 29	14·4	5·13	70	228·0	6·5	18·5	12·0	65·0

4. *Thuja (Biota) orientalis.*

26. iii. 29	14·0	6·05	50	117·0	6·5	6·0	—	0
26. iii. 29	11·0	4·49	51	113·0	7·0	2·5	—	0
10. vi. 29	29·5	16·83	38	57·5	8·2	9·0	0·8	9·0
6. vii. 29	26·2	12·07	35	75·5	11·0	12·0	1·0	9·0
13. vii. 29	20·2	9·77	55	227·5	13·4	12·5	—	0
6. viii. 29	27·4	11·63	35	52·0	6·9	6·5	—	0

5. *Thuja occidentalis.*

22. iii. 29	7·3	3·24	32·0	86·0	2·0	2·0	0·0	0
10. vi. 29	29·5	16·83	46·0	89·5	17·1	18·0	0·9	5·00
28. vi. 29	25·7	10·22	48·0	66·0	6·2	6·5	0·3	5·00
11. vii. 29	20·6	9·28	23·2	47·5	7·6	8·6	1·0	11·60
5. viii. 29	26·7	11·30	35·0	76·0	11·0	11·8	0·8	6·80
13. ix. 29	26·0	12·35	40·0	77·5	17·9	22·5	4·6	20·45
30. ix. 29	14·4	5·13	36·0	78·5	10·0	10·6	0·6	6·00

II. Immergrüne Laubhölzer.

6. *Buxus sempervirens.*

29. iii. 29	14·65	5·27	61·0	92·0	1·3	1·0	—	0
12. vi. 29	28·0	16·32	70·0	110·5	9·8	14·0	4·2	30·00
27. vi. 29	26·7	12·34	40·0	50·5	1·3	4·5	3·2	75·00
6. vii. 29	30·2	13·97	70·0	151·0	11·8	13·0	1·2	9·00
20. vii. 29	24·7	11·04	60·0	91·0	6·1	9·5	3·4	45·20
31. vii. 29	27·1	14·17	54·0	137·0	11·8	16·1	4·3	26·50
14. viii. 29	25·7	9·16	75·0	238·0	13·5	19·5	6·0	30·80
5. x. 29	18·7	6·63	55·0	156·5	9·5	6·1	—	0

7. *Prunus laurocerasus.*

29. iii. 29	14·65	5·27	55·0	58·0	2·6	2·0	—	0
8. vi. 29	26·25	12·43	68·0	87·0	18·9	21·9	3·0	13·90
27. vi. 29	26·7	12·34	56·0	168·0	20·4	24·7	4·3	17·50
9. vii. 29	26·0	14·12	50·0	63·0	11·4	12·0	0·6	5·00
29. vii. 29	25·3	12·12	50·0	51·5	5·2	6·0	0·8	10·30
31. vii. 29	27·8	14·47	50·0	58·5	10·0	10·6	0·6	6·00
15. viii. 29	29·2	12·82	65·0	49·0	7·7	9·7	2·0	20·60
26. ix. 29	15·6	5·82	40·0	57·5	1·9	1·0	—	0

III. Sommergrüne Laubhölzer (mit stark schwankendem Wasserverbrauch, während der Trockenzeit auch mit erheblicher Unterbilanz).

8. *Fraxinus oxicarpa.*

(1) Tag des Versuchs	(2) Temperatur in ° C.	(3) Sättigungs- defizit	(4) Länge des Zweiges in cm.	(5) Gewicht des Zweiges in gr.	(6) Menge des absor- bierten Wassers in gr.	(7) Menge des tran- spirierten Wassers in gr.	(8) Unter- bilanz in gr.	(9) Unter- bilanz in %
8. vi. 29	26·2	12·43	60·0	164·0	3·1	13·5	10·4	80·00
25. vi. 29	26·7	12·54	50·0	151·5	5·1	9·5	4·4	57·00
9. vii. 29	26·0	14·12	45·0	127·0	1·3	6·5	5·2	80·00
13. vii. 29	20·2	9·77	65·0	134·5	1·7	6·0	4·3	71·00
26. vii. 29	26·8	15·65	57·0	122·5	2·0	4·5	2·5	55·50
7. viii. 29	26·7	12·79	30·0	106·5	1·2	5·5	4·3	78·20
23. ix. 29	16·7	6·32	30·0	57·0	0·9	5·1	4·1	82·00
4. x. 29	18·5	6·59	23·0	51·5	0·4	4·5	4·1	91·10

9. *Fraxinus excelsior.*

1. vi. 29	17·0	5·32	60·0	95·0	2·2	8·0	5·8	70·25
12. vi. 29	28·0	16·32	70·0	180·0	3·0	10·0	7·0	70·00
26. vii. 29	26·8	15·65	85·0	153·0	2·1	7·0	4·9	70·00
31. ix. 29	16·7	6·32	43·0	101·5	2·4	19·0	16·6	88·50
4. x. 29	18·5	6·59	18·0	82·0	0·8	11·5	10·7	93·00

10. *Morus alba.*

7. vi. 29	25·0	13·47	80·0	87·0	5·9	9·0	3·1	34·50
2. viii. 29	28·3	15·34	85·0	52·5	9·0	10·1	1·1	10·90
17. ix. 29	17·0	3·30	90·0	70·5	26·4	26·2	—	0

11. *Gleditschia triacanthos.*

11. vi. 29	30·25	16·29	95·0	102·0	4·5	10·5	6·5	60·00
19. vi. 29	25·2	11·37	78·0	165·0	4·5	9·5	5·0	52·00
8. vii. 29	28·0	15·10	70·0	142·5	5·5	10·0	4·5	45·00
18. vii. 29	26·0	15·21	90·0	119·0	3·4	10·0	6·6	66·00
1. viii. 29	27·8	13·96	70·0	151·5	4·4	11·0	6·6	59·50
7. viii. 29	26·7	12·79	65·0	168·5	4·4	11·1	6·7	60·40
13. viii. 29	27·5	16·67	106·0	172·0	4·2	2·0	—	0
27. ix. 29	13·8	5·04	100·0	223·0	10·0	16·0	6·0	38·00 ·

12. *Juglans regia.*

5. vi. 29	24·2	14·35	70·0	230·0	15·1	24·5	9·4	38·30
5. vii. 29	28·5	13·75	55·0	255·0	20·5	23·0	2·5	10·90
22. vii. 29	25·2	12·67	25·0	136·0	9·0	10·0	1·0	10·00
2. viii. 29	28·3	15·34	30·0	171·0	7·3	9·8	2·5	25·50
20. viii. 29	30·0	17·75	57·0	107·0	8·5	22·0	13·5	61·30
7. ix. 29	21·7	8·24	62·0	99·5	6·5	10·4	3·9	37·50
20. ix. 29	22·5	12·23	20·0	92·0	24·2	26·2	2·0	7·60

13. *Robinia pseudoacacia.*

11. vi. 29	30·2	16·19	70·0	90·5	39·2	44·3	5·1	11·30
1. vii. 29	24·5	10·97	75·0	149·0	43·0	47·4	4·4	9·30
23. vii. 29	25·3	12·12	85·0	221·0	10·5	22·5	12·0	53·30
8. viii. 29	26·5	12·25	53·0	109·0	28·6	28·8	0·2	0·70
16. viii. 29	28·2	12·41	92·0	151·0	12·2	16·0	3·8	24·00
17. ix. 29	17·0	3·30	60·0	101·0	9·2	7·6	—	0

14. *Acer pseudoplatanus.*

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Tag des Versuchs	Temperatur in ° C.	Sättigungs-defizit	Länge des Zweiges in cm.	Gewicht des Zweiges in gr.	Menge des absorbierten Wassers in gr.	Menge des tran. spirierten Wassers in gr.	Unterbilanz in gr.	Unterbilanz in %
31. v. 29	20·75	6·98	97·0	101·5	20·0	25·0	5·0	20·00
12. vi. 29	28·0	16·32	64·0	69·0	12·9	17·0	4·1	24·70
15. vi. 29	27·6	13·26	106·0	183·0	15·0	23·7	8·7	36·60
15. vi. 29	27·6	13·26	80·0	87·0	20·0	27·0	7·0	26·00
15. vi. 29	27·6	13·26	68·0	82·5	26·0	31·3	5·3	17·00
29. vi. 29	24·5	11·21	56·0	83·5	16·2	18·5	2·3	12·40
29. vii. 29	25·9	14·44	90·0	220·0	30·7	31·0	0·3	0·90
8. viii. 29	26·5	12·25	75·0	194·0	50·1	51·0	0·9	1·79
19. ix. 29	22·3	10·9	50·0	99·0	26·2	24·1	—	0

IV. Sommergrüne Laubhölzer (mit schwach schwankendem Wasserverbrauch und mit unerheblicher Unterbilanz während der Trockenzeit).

15. *Alnus glutinosa.*

25. vi. 29	26·7	12·54	70·0	92·0	71·5	73·3	1·8	2·45
10. vii. 29	21·2	9·28	90·0	111·0	35·8	36·3	0·5	1·30
10. vii. 29	21·2	9·28	80·0	73·0	19·5	19·6	—	0
15. vii. 29	29·2	12·82	112·0	158·4	9·0	18·0	9·0	50·00
26. ix. 29	15·6	5·82	65·0	48·5	13·6	13·5	—	0

16. *Castanea vesca.*

8. vi. 29	26·25	12·43	95·0	223·0	64·4	65·4	1·0	1·50
6. vii. 29	30·2	13·97	90·0	206·5	32·0	35·5	2·5	7·10
20. vii. 29	24·7	11·04	90·0	197·0	25·0	25·0	—	0
21. ix. 29	25·0	11·64	80·0	203·5	72·3	72·3	—	0

17. *Acer dasycarpum.*

18. vi. 29	25·2	9·82	88·0	66·3	9·3	8·5	—	0
4. vii. 29	27·5	13·02	70·0	75·0	25·7	26·5	0·8	3·0
19. vii. 29	24·5	15·75	120·0	170·0	27·1	29·5	2·4	8·1
26. vii. 29	26·8	15·65	53·0	62·0	9·8	8·6	—	0
7. viii. 29	26·7	12·79	60·0	52·5	9·4	8·4	—	0
1. x. 29	24·9	6·18	45·0	50·5	7·5	8·2	0·7	8·5

18. *Carpinus betulus.*

8. vi. 29	26·2	12·43	103·0	91·0	27·6	30·0	2·4	8·0
15. vi. 29	27·6	13·26	—	241·5	93·5	96·0	2·5	2·6
19. vi. 29	25·2	11·37	95·0	182·5	72·3	72·0	—	0
29. vi. 29	24·5	11·21	90·0	171·5	44·0	54·5	10·5	20·0
18. vii. 29	26·0	15·21	90·0	149·0	56·0	54·5	—	0
29. vii. 29	25·9	14·44	86·0	78·0	22·2	21·8	—	0
10. viii. 29	27·2	12·64	60·0	44·0	6·9	5·9	—	0
1. x. 29	24·9	6·18	70·0	55·0	15·4	15·5	0·1	0·7

19. *Acer platanoides.*

5. vi. 29	24·25	14·35	78·0	98·0	9·3	7·0	—	0
20. vi. 29	26·7	11·18	80·0	164·0	15·3	16·0	0·7	4·4
3. vii. 29	25·0	11·32	80·0	204·0	20·4	15·8	—	0
22. vii. 29	25·2	12·67	77·0	219·0	18·5	14·0	—	0
30. vii. 29	25·7	10·45	43·0	63·0	4·9	3·7	—	0
9. viii. 29	26·1	11·12	70·0	68·5	7·7	6·2	—	0
19. ix. 29	22·3	9·24	40·0	82·0	35·4	37·6	2·2	6·0

20. *Fagus silvatica.*

(1) Tag des Versuchs	(2) Temperatur in ° C.	(3) Sättigungsdefizit	(4) Länge des Zweiges in cm.	(5) Gewicht des Zweiges in gr.	(6) Menge des absorbierten Wassers in gr.	(7) Menge des tranpirierten Wassers in gr.	(8) Unterbilanz in gr.	(9) Unterbilanz in %
8. vi. 29	26·2	12·43	110·0	196·0	9·5	9·5	—	0
21. vi. 29	22·0	5·87	94·0	110·0	6·2	5·5	—	0
6. vii. 29	30·2	13·97	70·0	80·5	12·5	12·0	—	0
20. vii. 29	24·7	11·04	70·0	61·5	5·0	6·0	1·3	10·0
1. viii. 29	27·8	13·96	76·0	79·0	12·7	12·4	—	0
15. viii. 29	29·2	12·82	93·0	92·0	8·8	8·8	—	0
21. ix. 29	25·0	11·64	75·0	65·0	26·7	28·0	1·3	4·65

21. *Tilia argentea.*

5. vi. 29	24·2	14·35	68·0	291·5	45·0	43·0	—	0
3. vii. 29	25·0	11·32	53·0	76·0	20·6	21·2	0·6	2·8
17. vii. 29	25·2	13·69	70·0	193·0	24·6	23·2	—	0
27. vii. 29	28·0	15·32	80·0	175·5	15·5	14·7	—	0
9. viii. 29	26·1	10·47	70·0	201·0	19·9	17·0	—	0
24. ix. 29	14·7	6·12	67·0	198·0	8·3	5·8	—	0
4. x. 29	18·5	6·59	65·0	200·5	12·5	10·5	—	0

22. *Populus alba.*

7. iv. 29	25·0	13·47	100·0	192·0	47·8	45·5	—	0
15. vi. 29	27·6	13·26	76·0	164·0	69·8	70·7	0·2	0·3
1. vii. 29	24·5	10·97	110·0	232·0	103·0	106·0	3·0	2·83
23. vii. 29	25·3	12·12	110·0	231·0	31·8	32·5	0·7	2·15

23. *Quercus robur.*

4. vi. 29	23·75	15·32	70·0	87·0	67·5	76·5	8·5	11·20
20. vi. 29	26·7	11·18	75·0	228·0	21·0	19·0	—	0
3. vii. 29	25·0	11·32	75·0	234·0	46·7	51·7	5·0	9·60
15. vii. 29	21·5	9·92	90·0	219·5	58·3	58·3	—	0
30. vii. 29	25·7	10·45	60·0	180·5	18·1	17·5	—	0
10. viii. 29	27·2	12·64	75·0	178·0	15·2	14·7	—	0

24. *Quercus cerris.*

5. vi. 29	24·2	14·35	100·0	104·6	22·4	24·0	1·6	6·66
20. vi. 29	26·7	11·18	70·0	234·0	50·5	54·5	4·0	7·30
3. vii. 29	25·0	11·32	75·0	182·5	25·8	22·8	—	0
15. vii. 29	21·5	9·92	90·0	192·5	23·7	17·6	—	0
30. vii. 29	25·7	10·45	70·0	163·5	20·6	18·7	—	0
10. viii. 29	27·2	12·64	45·0	186·0	19·9	20·9	—	0
4. ix. 29	28·6	14·14	73·0	154·5	55·7	52·0	—	0

25. *Quercus rubra.*

31. v. 29	20·7	6·98	85·0	203·5	54·6	57·0	2·4	4·20
14. vi. 29	28·2	15·1	80·0	119·0	26·7	27·3	0·6	2·16
19. vi. 29	25·2	11·37	55·0	64·5	5·1	5·0	—	0
19. vi. 29	25·2	11·37	70·0	107·5	11·6	10·2	—	0
19. vi. 29	25·2	11·37	110·0	211·5	15·7	14·5	—	0
29. vi. 29	24·5	11·21	70·0	81·0	16·1	16·5	0·4	2·42
19. vii. 29	24·5	15·75	87·0	208·5	30·0	30·5	0·5	1·64
13. viii. 29	27·5	16·67	82·0	79·0	39·2	42·5	3·3	8·00
12. ix. 29	25·8	11·82	95·0	183·5	33·8	32·0	—	0
1. x. 29	24·9	6·18	100·0	214·0	24·7	24·7	—	0

26. *Ulmus campestris.*

1. vi. 29	17·0	5·32	100·0	132·0	17·0	12·5	—	0
20. vi. 29	26·7	11·18	90·0	160·0	29·6	27·0	—	0
15. vii. 29	29·2	12·82	92·0	56·0	51·4	55·3	3·9	7·00
7. ix. 29	21·7	8·24	112·0	84·5	29·9	31·7	1·8	5·68
12. ix. 29	25·8	11·82	55·0	59·0	8·9	8·9	—	0
24. ix. 29	14·7	6·12	78·0	46·5	9·8	9·3	—	0

THE ECOLOGY OF BUTTERBY MARSH, DURHAM

By BENJAMIN MILLARD GRIFFITHS, D.Sc., F.L.S.

(With Plate XVII, five Maps and three Sections in the Text.)

CONTENTS.

I. THE HABITAT.

BUTTERBY Marsh lies two miles south of the City of Durham at Low Butterby, a remote spot beside the River Wear, two miles north-east of the village of Croxdale. The marsh occupies the bed of a former loop of the River Wear, whose course at this point is very tortuous (see Map 1). The neck of the loop is only 70 yards wide, and the northern bend of the loop reaches to within 100 yards of the lower course of the river at Low Butterby. The river-valley is a plain half a mile wide and bounded by fairly steep escarpments. The plain was always liable to serious floods (see Surtees, **8**, p. 96 and footnote), and to counteract this, a new channel was cut across the neck of the loop. On a map of Low Butterby in the possession of Lt.-Col. H. C. J. Salvin of Croxdale Hall there is a written note stating that the operation of turning the river was carried out in 1811. Surtees (**8**, p. 96) says that the Burnhall estate, which formerly included the land within the loop, was added to the Croxdale estate in 1806. Greenwood's map of 1820 (Greenwood, **3**) shows the loop cut off, so that the date 1811 may be considered correct. The construction of the embankments, which finally cut the loop off from communication with the main river channel, probably took place during the next twenty years, probably after Low Butterby had been added to the Croxdale estate in 1820 (see Surtees, **8**, p. 110; p. 96 footnote).

Over most of its course the Wear is a fairly rapid river, but at Butterby the river was very slow. Hutchinson (**5**, p. 325), writing before 1787 says: "On the more distant side of the estate (of Low Butterby) the river flows deep and slow, forming a canal a mile in length where the adjacent lands make a considerable plain." Surtees (**8**, p. 109) says: "The southern reach of the Wear assumes a rather unusual character, flowing for near a mile dark, deep and slow in sullen sedgy majesty through pools haunted by heron." The cutting of the new channel in 1811 would probably not greatly alter the character of the old channel, because at first there would be no difference in level and the water would flow through both channels. A much greater change
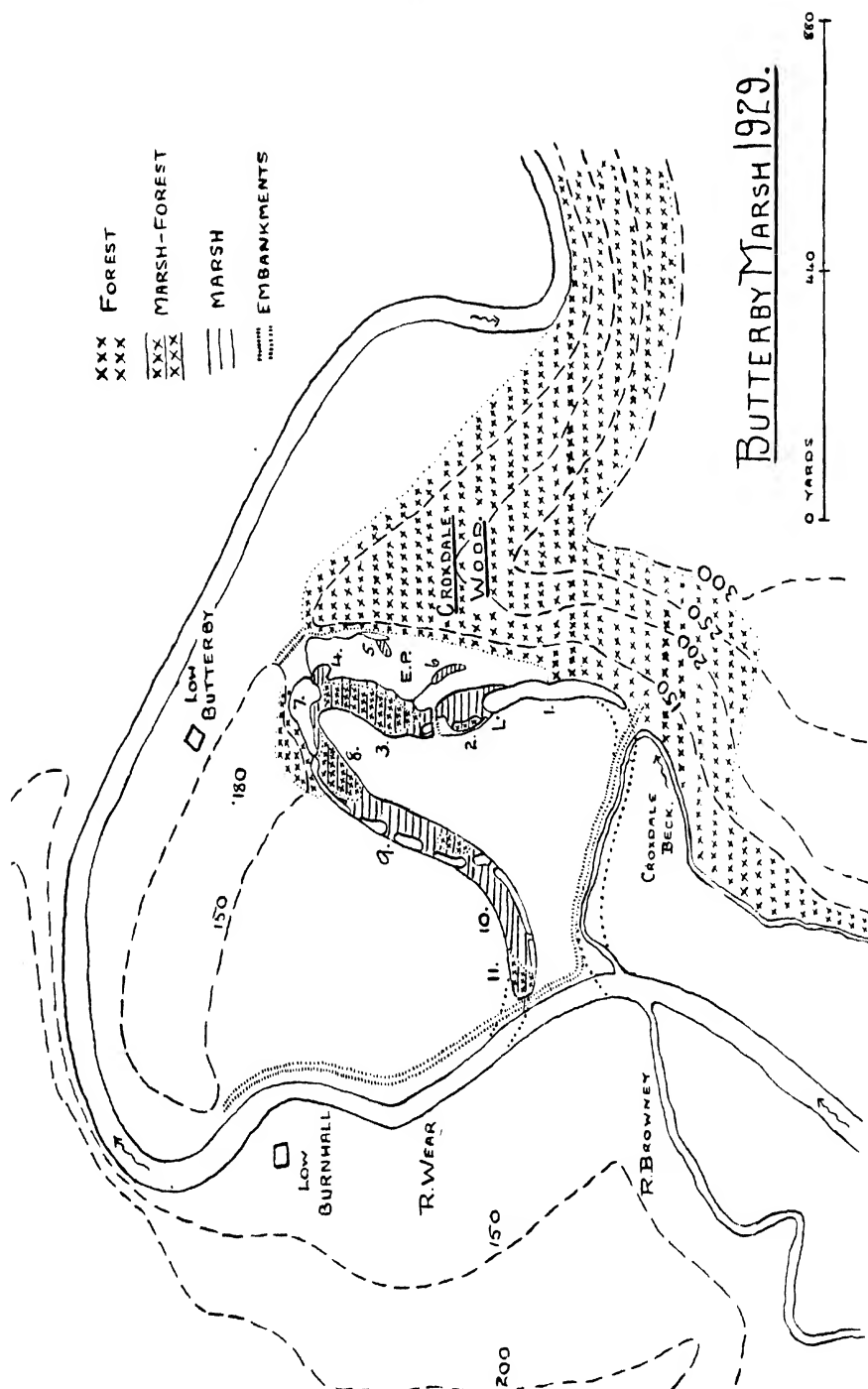
Map 1. General map of Butterby Marsh and district: contours shown by broken lines, drained parts of old loop shown by dotted lines. 1, Long Pool. 2, Typha Marsh: L, Laboratory; E.P., East Pasture. 3, East Salix Marsh. 4, Iris Marsh. 5, Woodside Marsh. 6, Middle Pasture Marsh. 7, Boathouse Pool. 8, West Salix Marsh. 9, Great Rumex Marsh. 10, Phragmites Marsh. 11, South Salix Marsh.

would occur when the embankments were made after 1820, when the current through the loop was stopped and the channel of the loop became a long back-water. The greatest change would be caused by the erosion of the bed of the river by the quickening of the current which the shortening of the course would bring about, and the consequent fall in the water level of the backwater in the loop. At the present day the surface of the river is nearly 6 ft. below the level of the outlet of the culvert which drains the marsh. The southern arm of the loop is completely drained, and the Croxdale Beck has cut a deep channel down into the old bed. The drainage of the rest of the loop was only partial, owing to the great irregularities in the depth of the bed, and it is this portion which is the Butterby Marsh of to-day. The former character of the marsh is indicated on the Ordnance Survey Map (25 inch, Durham, sheet xxvii, 9) by the fact that the boundary between the parishes of St Oswald's and Shincliffe still runs along the middle line of the old loop and not along the present course of the river.

In former times the land lying between the east arm of the loop and the eastern escarpment of the valley (East Pasture, E.P. Map 1) must have been for the most part under water, and the small marshes which now lie in it must have been very much more extensive.

The marsh now consists of a series of pools and marshlands, a good deal of the latter showing well-developed marsh forests or swamp carr (see Map 2 (inset), Map 5, and Pl. XVII, Phots. 2, 3, 4). The total area of the marsh is sixteen acres, of which twelve are marshland and four are pools. The marsh is three-quarters of a mile long, and varies in width from 86 to 220 ft. The Boathouse Pool reaches a depth of 14 ft.; the Long Pool, 10 ft. The marsh is divided into two unequal parts by a short transverse embankment across the middle of the eastern arm of the loop. The embankment gives communication between the arable land within the loop (called "the Island" on Ord. Survey Map), and the East Pasture. The culvert under the embankment has become blocked and the upper part of the marsh does not communicate with the lower. There is a difference of 1 ft. 2 in. between the overflow levels of the two sections of the marsh. The upper marsh overflows into the lower marsh during late winter and the spring.

The inner banks of the channel of the marsh are fringed with Salices, but the outer banks are nearly free from trees except where Croxdale Wood and the Boathouse Wood come down to the edge of the marsh. The fringing trees are mostly *Salix fragilis* but there also occur *Alnus rotundifolia, Salix alba, S. pentrandra, S. Andersoniana (S. nigra), S. viminalis, S. purpurea,* and many hybrid Salices of which *S. purpureus × viminalis* is perhaps the commonest.

The marsh forest consists of *Alnus rotundifolia, Salix alba, S. fragilis* and *S. cinerea.*

The dominant herbaceous plant of the Marsh is *Rumex hydrolapathum,* which is a rare plant in Co. Durham, but occurs here in the greatest profusion.

Phragmites communis is dominant at the far end of the marsh. *Scirpus lacustris* is very scarce and only occurs as a small patch at the north end of the Long Pool. *Nuphar luteum* is abundant in the Long Pool, the Boathouse Pool and in some of the deeper, small and narrow pools in the northern arm of the marsh.

The inner bank of the marsh is usually steep, and varies in height from 7 ft. 9 in. to 5 ft. 6 in. above high-water mark. Its slope is often covered with *Petasites vulgaris*. The outer bank is lower and has a more gentle slope. It varies in height from a few inches to 3 ft. 6 in. or 4 ft. above high-water mark.

The water supply of the marsh is scanty but uncontaminated. It is derived entirely from the rainfall on the west slope of Croxdale Wood, the west slope of the 180 ft. ridge which runs across the river plain, and from the land within the loop. The total catchment area is only about 120 acres. No water enters the marsh from the river or from the Croxdale Beck, both of which are much polluted with coal washings, pit water, coke-oven effluent and sewage. The small water supply is insufficient to maintain the water of the marsh at a constant level, and there are large but fairly regular fluctuations. In 1928 and 1929 the marsh was full and overflowing from February to April or May, but after May the level sank steadily until October and then rose steadily to overflow level by February. In 1930, however, the level fell from May only until July and then rose to overflow level again in August, at which point it has been maintained to date (October, 1930). In 1927 and 1928 the seasonal fall in level was 2 ft., but in the dry year 1929 the fall was 2 ft. 9 in., and in the wet year of 1930 the fall has only been 9 in. The extreme variations in level affect the vegetation of the following season. The drought of 1929 was followed in 1930 by a great spread of *Oenanthe Phellandrium* in the Typha Marsh, *Ricciocarpus natans* almost completely disappeared, and *Typha* did not come into flower at all.

The marsh as a whole is a neutral-water habitat. The prevalent mosses are *Mnium affine* var. *elatum* and *Hypnum fluitans* var., and no *Sphagnum* or *Polytrichum* occur. The water which flows into the Long Pool from Croxdale Wood has a reaction of pH 8·5 (B.D.H. Universal Indicator). The water of the pools of the marsh is about neutral, pH 7·0–7·5, e.g. Long Pool, Boathouse Pool, Woodside Marsh Pool, and the deeper of the narrow pools in the northern arm of the marsh. The water of the outflow at the far end of the marsh is also pH 7·0–7·5. The Typha Marsh, the Iris Marsh, and the smaller and shallower pools tend to have water of pH 6·5–7·0. The water in the society of *Salix cinerea* at the south end of the East Salix Marsh is 6·5, and the same reaction was found in the water of the isolated society of pure *Equisetum limosum* on the west side of the East Salix Marsh.

The surface layers of the soil of the river plain through which the channel of the marsh runs, are composed of sandy clay silts almost entirely devoid of pebbles. Sections through the deposits of the river plain are to be seen in the

south arm of the loop where the Croxdale Beck has cut a deep channel down through the beds. The sections show 5 or 6 ft. of sands and clay-silts above, passing down into coarse sand and pebble beds below. The vegetation of the marsh, however, does not grow directly on the clay silt but on a layer of autochthonous organic detritus which varies from 9 in. to as much as 2 ft. in thickness. The upper layer of the detritus contains more or less recognisable fragments of the vegetation from amongst which the sample of detritus was taken, but the lower layers consist of minute amorphous particles, dark brown, grey or black in colour, forming a black mud. Among the *Rumex* plants at the south end of the East Salix Marsh (see also p. 126) and at the south end of the Typha Marsh, the detritus is about 9 in. thick; among the *Nuphar* plants in the Long Pool the thickness is about a foot; in the middle of the *Typha* society in the Typha Marsh the mud is from 1 ft. 6 in. to 2 ft. thick. By means of a mud sampler of special design, it was found that the black mud layer of the Typha Marsh overlay a stratum of grey clay 3 ft. thick, passing down into yellow silty clay 1 ft. 6 in. thick. Below this lay pebble beds which the mud sampler was unable to penetrate. The layer of grey clay contained abundant fragments of the rhizomes, roots and shoots of *Equisetum limosum*, but they were absent from the yellow clay silt. As *Equisetum* does not occur in the present surface layer of black mud, the grey clay stratum probably represents a former surface of the floor of the marsh which was covered with *Equisetum* (see p. 126). The succession of sediments underneath the Typha Marsh is not the same as that of the river plain through which the channel of the marsh runs. The sediments which fill the channel of the marsh, namely clay and clay silt, have probably been deposited from the water of the river when the rate of flow of the current was diminished on entering the long and almost level reach of the old loop.

II. THE DISTRIBUTION OF THE VEGETATION, 1929.

There do not appear to be any local names for the different regions of the marsh, and those used in the following account are invented by the writer. The nomenclature is based mainly on the dominant species of the consociations into which the marsh association can be divided.

The marsh is naturally divided into two parts by the transverse embankment, namely the Upper Marsh and the Lower Marsh, but the subdivisions of the two are only for convenience of description. The regions which may be distinguished are:

A. Butterby Upper Marsh: 1, the Long Pool; 2, the Typha Marsh.

B. Butterby Lower Marsh: 3, the East Salix Marsh; 4, the Iris Marsh in the East Pasture; 5, the Woodside Marsh in the East Pasture; 6, the Middle Marsh in the East Pasture; 7, the Boathouse Pool; 8, the West Salix Marsh, including the Alnus Forest Marsh; 9, the Great Rumex Marsh; 10, the Phragmites Marsh; 11, the South Salix Marsh.

A. *Butterby Upper Marsh.*

1. *The Long Pool* (Map 2; Section 1).

Area 2·27 acres; width from 86 to 100 ft.; length 900 ft.; greatest depth 10 ft. The south end of the pool is much shaded by a fringe of willows on the west bank and by alders on the east bank where Croxdale Wood comes down to the water's edge, but the north end is almost free from trees. At the north end the pool is abruptly bounded by the *Rumex hydrolapathum* fringe of the Typha Marsh. The littoral marsh vegetation of the pool is relatively scanty, owing to the steepness of the slope of the banks at the north end, and possibly owing to the shading effect of the trees at the south end where the slope of the banks is low. At the south end of the pool there is a complex community on the west bank, consisting of *Digraphis arundinacea* and *Carex paludosa*, together with a very small reed swamp of *Phragmites communis* and *Typha latifolia.* Behind the consociation lies a small marsh forest of *Salix Andersoniana.* Further north on the same side, there are two societies of *Phragmites* and a long and narrow society of *Carex paludosa*, in which are a few trees of the hybrid willow *Salix viminalis* × *purpurea.* Adjacent to the *Rumex* fringe there is a small society of *Scirpus lacustris* lying 2 ft. 6 in. below overflow level or high-water mark[1]. This is the only station for the plant in the marsh. The more northerly of the *Phragmites* reed swamps is practically pure, but the other one mingles with *Caltha palustris* and *Digraphis* on its landward edge. Both communities descend to a depth of 2 ft. 6 in. below h.w.m. and are succeeded immediately by *Nuphar luteum.*

The scale of the map does not permit the indication of zones of less than 2 or 3 ft. in horizontal width, and consequently the zonation of the vegetation on the steeper banks cannot be shown. Thus the society of *Carex paludosa* on the west bank has a thin line of *Digraphis* behind and a thin and broken line of *Rumex hydrolapathum* in front; the apparently bare bank of the middle east shore is zoned as follows from above downwards: *Juncus glaucus, Digraphis, Rumex* and *Equisetum limosum.* Section 1, on p. 112, is drawn on a larger scale than the maps, and the zonation of the vegetation is shown in greater detail.

The west bank adjoins the arable land which lies within the old loop of the river. The slope of the bank is steep and is covered with *Petasites vulgaris,* grasses, and *Ranunculus Ficaria,* together with some *Adoxa moschatellina.* The marsh vegetation comprises the following zones from above downwards: (*a*) *Digraphis,* narrow and broken line; (*b*) *Carex paludosa,* in a zone from 1 to 4 ft. broad; (*c*) *Rumex hydrolapathum,* few and scattered, with occasional *Sparganium ramosum*; (*d*) *Nuphar luteum.* There is no *Juncus glaucus* on this bank. The *Nuphar* zone extends from 2 ft. 6 in. below h.w.m., to 7 ft. 6 in., after which there is nothing but bare mud.

---

[1] Overflow-level or high-water mark will be hereinafter indicated by the contraction h.w.m.
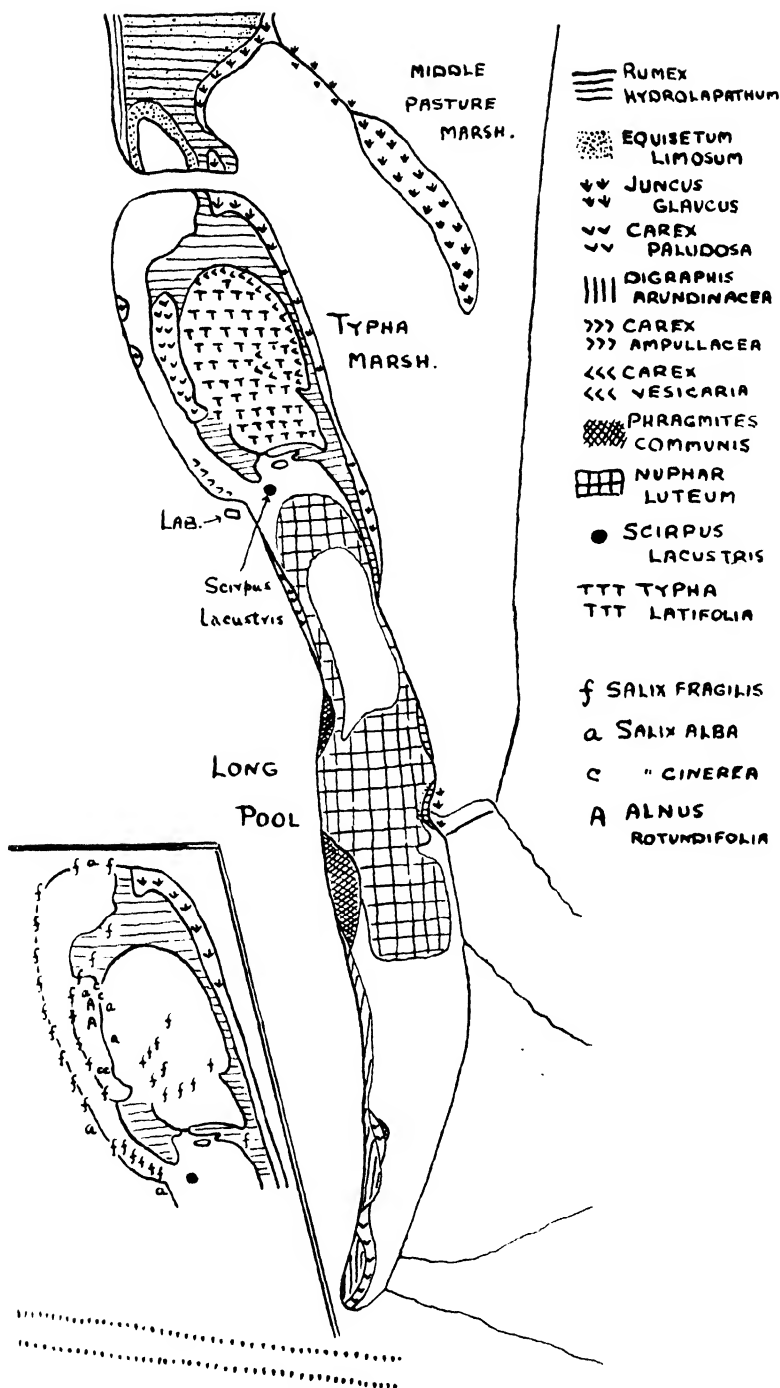
MAP 2. Long Pool, Typha Marsh, Middle Pasture Marsh: herbaceous vegetation. Inset map: dendrophytic vegetation of Typha Marsh; herbaceous vegetation partly omitted. Meaning of symbols shown on map.

The east bank lies on the edge of a well-grazed permanent pasture (the East Pasture), and the slope of the bank is lower than that of the west bank, and runs out westwards in a submerged shelf. The zonation from above downwards is:

(a) *Juncus glaucus*, occupying a zone some 9 ft. broad. In the upper part of the zone *Ranunculus Ficaria* is plentiful, and lower down there occur *Polygonum amphibium, Filipendula Ulmaria, Senecio aquaticus* and *Achillea Ptarmica*. The lower edge of the zone is much trampled by cattle, so that the surface of the ground is irregularly pitted with depressions which often lie at a lower level than the ground immediately in front, and which carry a flora appropriate to that level. The cattle-trampled zone is from 1 to 2 ft. wide.

(b) *Digraphis arundinacea*, occupying a zone about 1 ft. or 18 in. wide, but much broken by the trampling of cattle.
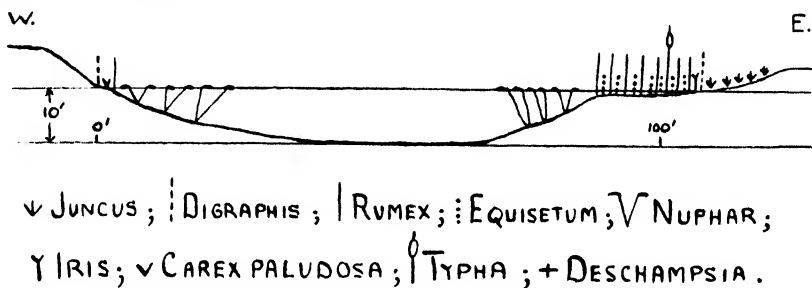
SECTION 1. Long Pool: east-west section at north end. Upper horizontal line shows high-water level; lower horizontal line is 10 ft. below h.w.l. The meaning of the symbols is shown on the Section. Vertical scale = horizontal scale.

(c) A community comprising *Caltha palustris, Scutellaria galericulata, Mentha aquatica, Valeriana officinalis, Lycopus europaeus, Myosotis palustris, Stellaria uliginosa*, and occasional *Eleocharis palustris, Juncus communis, Alisma plantago*, and *Oenanthe Phellandrium. Lemna minor* and *Ricciocarpus natans* are abundant on the surface of the water among the shoots of the rooted vegetation. Many plants of this community occur on the landward side of the *Digraphis* zone in the depressions made by the feet of the cattle.

(d) *Iris pseudacorus*, mingled with *Sparganium ramosum*, forming an irregular and broken zone.

(e) *Rumex hydrolapathum*, occupying a zone 18 ft. wide, and mixed with *Equisetum limosum* and occasional *Typha latifolia*. The zone ends abruptly at a level of 1 ft. below h.w.m. Beyond this point the ground drops suddenly to a depth of about 2 ft. 6 in. below h.w.m. There is no zone of pure *Equisetum limosum*, and the *Rumex* zone is followed immediately by *Nuphar*.

Further southwards the submerged shelf into which the bank is prolonged dies out, and the bank assumes a steeper and more uniform slope. The same zonation of vegetation is maintained on the steeper banks but in a more attenuated and broken form. The bank adjacent to Croxdale Wood projects

about 20 ft. into the pool. It consists of a fan or delta of silt which has been formed from the sediment carried into the pool by a drainage channel from the wood. The slope of the fan is less steep than that of the bank immediately northward of it, and is much more uniform than that of the submerged shelf. The zonation from above downwards is: *Juncus glaucus* community; cattle-trampled zone with *Caltha*, etc.; *Digraphis*; *Sparganium*; *Rumex* with *Equisetum*; pure *Equisetum*. The *Rumex* zone descends to a depth of 1 ft. 6 in. below h.w.m., and *Equisetum* to 2 ft. 6 in., where it is immediately followed by *Nuphar*, which descends to 7 ft. 6 in. below h.w.m.

Owing to the steep slope of the east and west banks of the pool, *Nuphar* comes in close to the shore, but at the north end there is a gap between the edge of the *Nuphar* society and the *Rumex* society, and there is a much larger unoccupied area at the south end of the pool. A very small amount of *Potamogeton crispus* occurs at the north end beyond the *Nuphar*, but at the tree-shaded southern end of the pool, the bottom is devoid of vegetation.

2. *The Typha Marsh* (Map 2).

Area 1·25 acres; the surface of the mud at the centre of the Typhetum is 2 ft. below h.w.m.; the *Rumex* society lies in about 1 ft. of water; the society of *Carex paludosa* lies just at h.w.m.; the channel on the west side is about 6 in. deep at the southern end and almost blocked by fallen willows, but northward the channel becomes deeper and ends in a small pool which is about 4 ft. deep.

The community lies in a kind of shallow saucer, the centre of which is occupied by *Typha latifolia*, most of the rim by *Rumex hydrolapathum*, and the highest part of the rim by *Carex paludosa*. A prolongation of the *Rumex* society extends some distance along the east side of the north end of the Long Pool.

The southern part of the Typhetum mingles to some extent with the *Rumex* zone, but the northern and larger part is pure. Around the northern, eastern and southern edge of the pure *Typha* there lies a very narrow but distinct zone of *Carex vesicaria* L. This is the only station in the marsh for *C. vesicaria*, but the closely allied *Carex ampullacea* Good. occurs in fair amount near the laboratory at the south-west corner of the Typha Marsh, and also on the edge of the *Alnus* forest in the East Salix Marsh, and in the South Salix Marsh. The pure Typhetum ends sharply at the *Carex vesicaria* zone on the north and does not penetrate the *Rumex* society. The latter is not pure, however, but is much mixed with *Juncus communis*, *Sparganium* and *Iris*, and passes rather indefinitely into the *Juncus glaucus* zone. The Upper Marsh overflows into the Lower Marsh over the lowest part of the transverse embankment at the north-east corner of the Typha Marsh. Frogs lay their eggs here in March.

There is a dense fringe of *Salix fragilis* on the west bank of the marsh,

extending from the laboratory to the transverse embankment (see Map 2, inset). The trees overshadow the channel which runs beside the west bank, and in several places the channel is partly blocked by fallen trees. The channel is only about 6 in. deep at the south end but becomes deeper as it passes northward. Between the channel and the Typhetum there extends a long and narrow "island" of *Carex paludosa*, on which is a small marsh forest or swamp carr (Map 2, inset). On the highest part of the island there are a few specimens of *Alnus rotundifolia* and *Salix alba*. *Salix fragilis* forms a fringe around them, and there are a few *S. cinerea* on the extreme north-east margin of the forest and also at the south end. The undergrowth of the forest consists of *Carex paludosa* together with *Scirpus sylvaticus*.

Within the limits of the Typhetum there is a group of dead or dying specimens of *Salix fragilis*, and other specimens occur in the *Rumex* zone at both the south and the north-west ends of the Typha Marsh. In addition there are two dying trees of *Salix alba* just beyond the edge of the *Carex paludosa* society on the north-east side. It is probable that the level of the water in the Upper Marsh has been raised by the stoppage of the culvert under the embankment, and the increase of depth has killed or is killing all those trees which formerly stood near the lower limit of the depth below h.w.m. which they could tolerate. There is a kind of cape of the *Rumex* projecting into the Typhetum from the southern east shore towards the group of dying and dead trees, and this may indicate a ridge of slightly higher ground which is now submerged. It is probable, however, that the death of the trees is not entirely due to submergence, but is due to submergence in stagnant water (see note on distribution of *Typha latifolia*, p. 122).

On the east bank of the Typha Marsh the distribution of the vegetation is almost identical with that of the east bank of the Long Pool, except that in the central portion of the bank the zones are very narrow and abut directly on the Typhetum. There are no trees on the east bank.

B. *Butterby Lower Marsh.*

The Lower Marsh is continuous from the Transverse Embankment to the outlet culvert at the western end of the channel. There are no fairly clear-cut natural divisions as in the case of the Upper Marsh, and the divisions adopted in the following description are made for the sake of convenience in treatment. The vegetation is similar to that of the Upper Marsh, but it is developed on a more extensive scale. Much of the area is forested, and *Equisetum limosum* plays a much bigger part in the communities.

Northward of the Transverse Embankment the channel of the marsh becomes broader, reaching a width of 230 ft. at the round reach of the Boathouse Pool, and maintaining a width of about 210 ft. for the rest of its course. At the Boathouse Pool the channel makes a sudden bend through an angle

of 130°. The change of direction is caused by the presence of the 180 ft. ridge, into which the old river cut and formed an escarpment some 40 ft. in height which is now covered by the Boathouse Wood. There is a small but constant spring in the wood, from which a brooklet runs into the North Bay of the Pool. The vegetation of the estuary forms a distinct community. The escarpment faces southward and the hill protects the pool from northerly winds. *Caltha* and *Iris* come into flower in the North Bay at least a week before those in the rest of the marsh, and the surface temperature of the Boathouse Pool is usually from one to two degrees Centigrade higher than in the Long Pool during the spring and autumn. On the other hand, when a strong south-west wind is blowing, the temperature of the Boathouse Pool drops below that of the Long Pool, because the former pool lies north-east to south-west and the wind sweeps along its length, but the Long Pool lies nearly north-south, and the wind blows across it.

3. *The East Salix Marsh* (Maps 3 and 5; Section 2; Pl. XVII, Phot. 2).

Area 3·56 acres; 220 ft. wide at broadest part. The west bank is steep and reaches a height of 7 ft. 6 in. above h.w.m. The slope is covered with *Petasites* in the middle section, but both the northern and southern sections are occupied by *Digraphis*. Most of the bank is fringed with *Salix fragilis*. *Carex distans* is frequent under the trees in the middle sections. The east bank has a low slope and is only 3 ft. 6 in. above h.w.m. There are no trees on the east bank and no *Digraphis*.
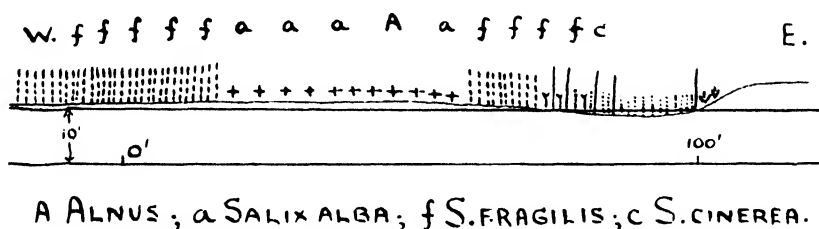
SECTION 2. East Salix Marsh: east-west section of eastern side of community.
Symbols for herbaceous vegetation as in Section 1.

The channel of the marsh is very shallow, and in the central part the floor rises to a height of about 6 in. above h.w.m. The central area of the channel is occupied by a large marsh forest. The ground vegetation consists of a central and higher "island" of *Deschampsia caespitosa*, surrounded by a wide zone of *Digraphis* which is mixed with *Scirpus sylvaticus*, *Mentha*, *Valeriana* and some *Caltha*. The forest trees on the *Deschampsia* area consist of *Alnus rotundifolia* and *Salix alba*; *Salix fragilis* occupies the area of *Digraphis*, but also spreads

northward, southward and to a lesser extent eastward into the surrounding community of *Rumex hydrolapathum* and *Equisetum limosum*. The small southern outlier of *Deschampsia* bears a specimen of *Viburnum opulus*. The zone of *S. fragilis* is followed by a zone of *S. cinerea* and hybrids between *S. cinerea* and *S. caprea* and *S. viminalis*. The zone of *S. cinerea* is entirely in the *Rumex-Equisetum* community. It is very extensively developed northward but less so southward (see Map 5).

The island of *Deschampsia* and *Digraphis* is surrounded with the *Rumex-Equisetum* community which extends without a break from the transverse embankment to the Boathouse Pool. At the south end the community is mixed with a good deal of *Iris* and *Sparganium*, but at the north end the *Sparganium* is replaced by scattered *Typha*. At the south end there is a small triangular pool containing *Potamogeton natans*. The *Rumex-Equisetum* community passes into pure *Equisetum* around the margin of the pool, and there is also a small society of *Equisetum* in a deeper part of the channel which lies between the *Digraphis* island and the west bank. On the south-west margin of the *Digraphis* island there is a small society of *Acorus calamus*. This plant is not recorded for Co. Durham either by Winch (9), Ornsby (6) or Baker and Tate (2), but it is easily overlooked among the *Iris* and *Rumex*. The channel on the eastern side of the *Digraphis* island is broad and shallow, and though *Equisetum* is fairly abundant within it, there is a considerable admixture of *Rumex*. *Juncus glaucus* fringes the low east bank of the marsh.

The marshes of the East Pasture.

The pasture field which lies between the channel of the marsh and the wooded eastern scarp of the valley is 8·5 acres in area and contains three small marshy areas within the irregularities of its surface. The pasture is good grazing land and is free from trees and bushes. The marshy areas all drain into the East Salix Marsh.

4. *The Iris Marsh* (Map 3).

This little marsh lies at the north end of the East Pasture. It is nearly separated from the East Salix Marsh by a small island of pasture ground (*P* on Map 3), and communicates with the marsh by two narrow and shallow channels of which the southern appears to be the chief. The Iris Marsh receives the drainage of the Woodside Marsh by a ditch which enters at the north-east corner. The marsh is ringed with a broad zone of *Juncus glaucus* mixed with *Senecio aquaticus*, *Polygonum amphibium*, *Myosotis palustris*, *Cardamine pratensis* and *Eleocharis palustris*. Next comes *Glyceria fluitans* and *Ranunculus Flammula*, and the centre of the marsh is occupied by a mass of *Iris*, mixed with a little *Rumex*, *Equisetum* and occasional *Juncus communis*. At the north end, the *Rumex-Equisetum-Typha* community of the East Salix

Marsh pushes in, but dies out and is replaced by *Sparganium* where the flow from the ditch of the Woodside Marsh enters.

5. *The Woodside Marsh* (Map 3).

The marsh lies on the north-east side of the East Pasture at the foot of the wooded escarpment of the valley. It consists of a long and shallow pool, about
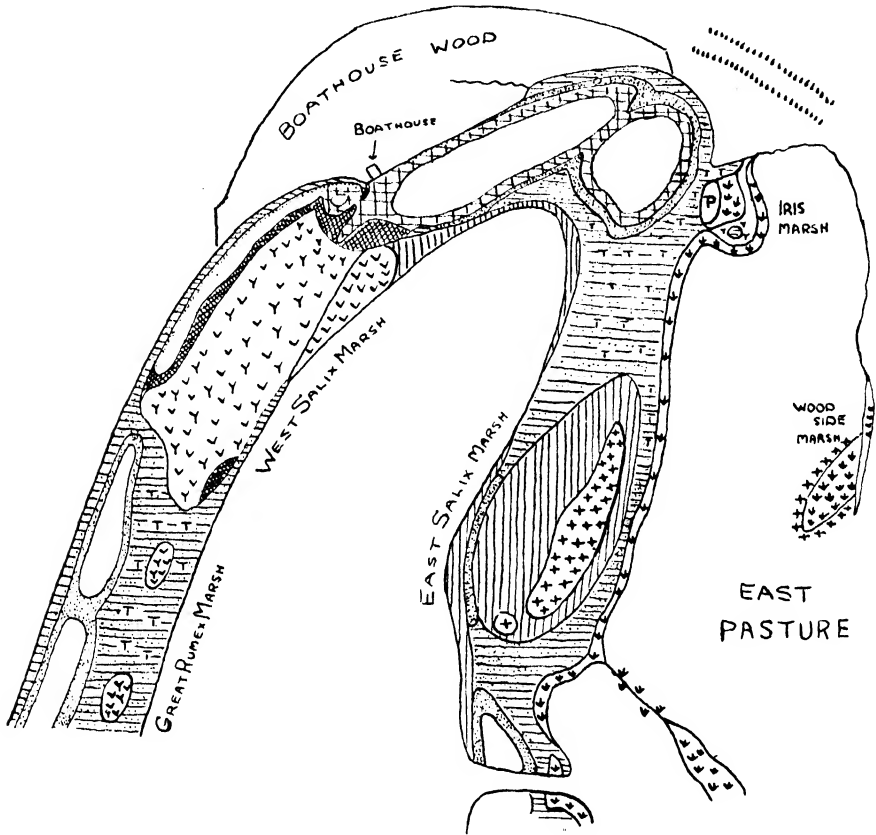
MAP 3. East Salix Marsh, Iris and Woodside Marshes, Boathouse Pool, West Salix Marsh, and northern part of Great Rumex Marsh: herbaceous vegetation. Symbols as in Map 2, with addition of Y *Iris*, and + *Deschampsia caespitosa*. *P* indicates an isolated part of the East Pasture.

100 ft. in length, 10 ft. in width and less than 1 ft. deep. There is some water in the pool at all seasons of the year. On the west side of the pool there is an area of marshland. The pool drains into the Iris Marsh, but the flow is seasonal.

The steep east bank of the pool is lined with a few groups of *Carex paludosa*, in front of which is a little *Rumex* and *Equisetum*. The deeper water contains *Potamogeton natans* and *Ranunculus aquatilis*. The very shallow west bank contains a little *Rumex*, together with *Oenanthe Phellandrium*, *Senecio aquaticus*,

Myosotis palustris, Glyceria and *Ranunculus sceleratus*. The marshland consists of *Juncus glaucus* with *Polygonum amphibium* and *Scutellaria galericulata*, surrounded by a fringe of *Deschampsia caespitosa*.

6. *The Middle Marsh* (Maps 2 and 3).

The marsh occupies the bottom of an elongated depression 275 ft. by 25 ft., lying 5 ft. 5 in. below the level of the pasture. It drains into the East Salix Marsh by a ditch 150 ft. long and 3 ft. wide. The depression probably represents a very old former channel of the river. The vegetation consists of *Juncus glaucus* mixed with a fair amount of *Scirpus sylvaticus*. Towards the centre of the marsh a few tufts of *Carex paludosa* occur and also a small amount of *Caltha* and *Glyceria*.
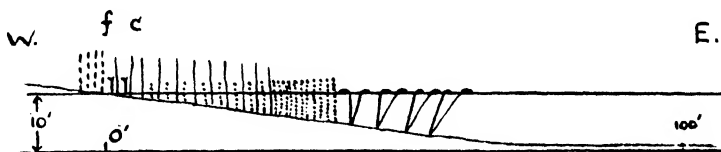
SECTION 3. Boathouse Pool: southwest-northeast section of west shore of round reach of the pool. Symbols as in Sections 1 and 2.

We now resume our account of the regions of the main channel of the Lower Marsh. The East Salix Marsh passes into

7. *The Boathouse Pool* (Maps 3 and 5; Section 3).

Area 1·23 acres; 9 ft. deep in the middle of the rounded southern reach, and 14 ft. deep in the elongated northern reach. The two reaches are separated by a subaqueous ridge whose lowest point is 5 ft. 6 in. below h.w.m. The pool shows the marsh vegetation in its fullest development. Section 3 shows the succession of zones from the middle of the round reach to the point of the great bend of the marsh. The complete succession from east to west is: *Juncus glaucus, Digraphis* and *Iris, Rumex-Equisetum* with *Salix cinerea, Rumex-Equisetum, Equisetum, Nuphar*[1] —— *Nuphar, Equisetum, Rumex-Equisetum, Rumex-Equisetum* with *Salix cinerea, Digraphis* and *Iris* with *Salix fragilis*. There is no *Juncus glaucus* zone on the west point; the *Digraphis* zone in the east bay is very narrow and broken. The west point adjoins arable land; the east bay is on the edge of a pasture field. *Rumex* extends to a depth of 1 ft. 6 in., *Equisetum* to 2 ft., and *Nuphar* to 7 ft. 6 in. The subaqueous ridge is marked by protrusions of *Rumex* and *Equisetum* and by a continuous line of *Nuphar*.

Castalia alba occurs in the round reach and at the south-west end of the long reach. It is stated to have been put into the pool by a former owner. It was there, however, before 1846, because Ornsby (**6**, p. 214) records "*Nymphaea alba*...in the old bed of the river at Butterby....Mr Peele."

[1] Only the western portion of the succession of zones is shown in the Section.

In the shallow bay on the north side of the pool, the inflow from the spring in the wood brings about a subsidiary formation within the normal zonation. The zonation of the estuary, from the landward side outwards, is: *Oenanthe crocata, Epilobium hirsutum*, pure *Equisetum*; the *Digraphis* and *Rumex* zones are absent. The estuarine vegetation forms a small triangle, but it is too small to be shown on the map.

At the south-west point of the north bay there is a zonation of *Deschampsia caespitosa, Juncus glaucus, Digraphis* and *Iris* with *Caltha, Rumex, Equisetum*. *Carex paludosa* occurs in a very narrow and broken zone from the point of the bay to the west end of the Boathouse Wood. The whole of this shore is fringed with *Salix fragilis*.

At the west end of the Boathouse Pool there is a conspicuous mass of *Phragmites communis*, forming the eastern fringe of the West Salix Marsh vegetation. The *Phragmites* occurs in two masses, nearly divided by a channel or inlet of deeper water. The southern mass is much penetrated by *Rumex* and *Equisetum*, but the northern mass is purer. Near the boathouse there is a narrow submerged ridge running obliquely across the channel, and the *Phragmites* has invaded it. At the south end, *Phragmites* occupies both sides of the ridge, but at the north end *Phragmites* occupies only the east side, and the west side is covered with the *Rumex-Equisetum* community. Westward of the ridge, there is a rounded pool 9 ft. deep and fringed with *Nuphar*. The pool is the end of the long channel which skirts the north side of the West Salix Marsh.

On the south bank of the long reach of the Boathouse Pool the *Rumex* zone suddenly becomes very narrow at the point where the *Alnus* forest begins, and then becomes broader again where it mingles with the southern *Phragmites* mass. The zone of *Equisetum* is more uniform.

8. *The West Salix Marsh* (Maps 3 and 5).

In this section of the marsh the communities become very complex. Their observation is rendered exceptionally difficult on account of the impassability of the marshy ground, the density of the willow forest and the obstruction of the view by fringes of *Phragmites* on the eastern and northern sides.

The communities are not arranged concentrically, as in the East Salix Marsh, but in the form of a curved fan whose focus or radiating point is situated on the south bank of the channel of the marsh almost immediately opposite the boathouse. At this point, the *Digraphis* zone which skirts the south bank becomes broader and passes over into a fan-shaped society of almost pure *Carex paludosa*. The broad part of the *Digraphis* zone and most of the society of pure *Carex paludosa* are covered with a forest of *Alnus rotundifolia*. On the northern edge of the *Alnus* forest there is a narrow fringe of *Carex ampullacea*, and under the alders *Carex distans* occurs.

Beyond the pure *C. paludosa* society, there stretches out a much larger

fan of *C. paludosa*, mixed with *Rumex, Equisetum* and much *Iris*. This mixed community spreads north-eastward and southward, and upon it there is a dense forest of *Salix fragilis* which has a small fringe of *S. cinerea* on the east side overlooking the Boathouse Pool, and a much larger fringe at the south end. The *Salix* forest ends abruptly on the east at the Boathouse Pool, and on the north at the long and narrow pool which represents the deeper part of the old channel of the river. The pool contains *Nuphar*. The east and north sides of
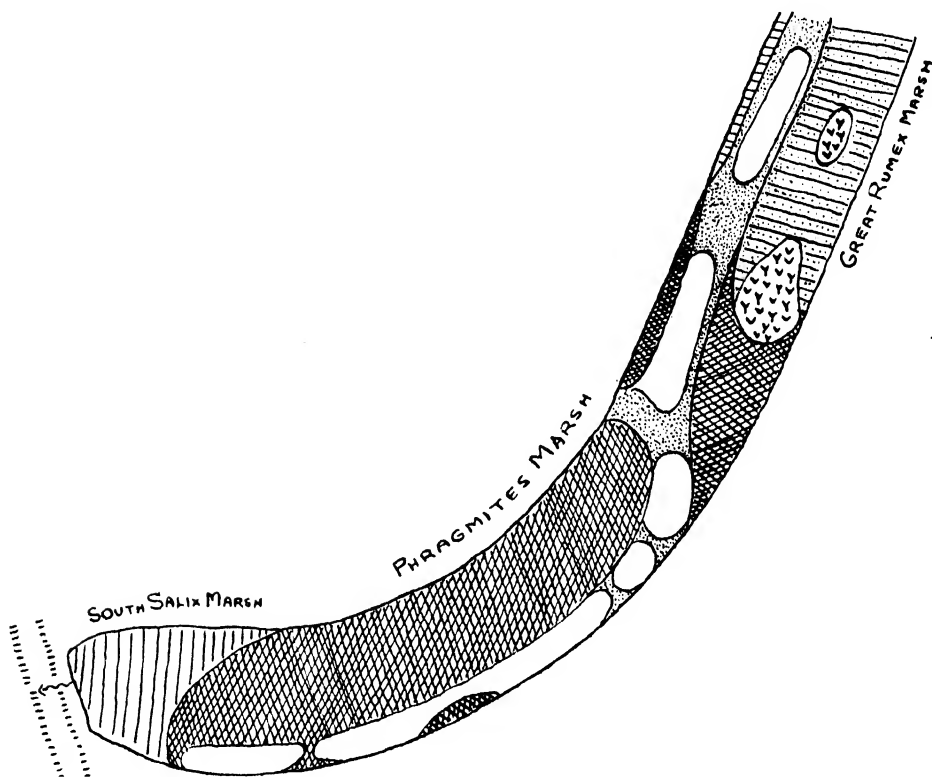
MAP 4. Southern part of Great Rumex Marsh, Phragmites Marsh and South Salix Marsh: herbaceous vegetation. Symbols as in Maps 2 and 3.

the forest are lined with a continuous zone of *Phragmites*. Towards the south, the *Salix* forest, with its fringe of *Phragmites*, passes into the Great Rumex Marsh. The northern zone of *Phragmites* invades and crosses the old channel at one point. There is a small impure aggregation of *Phragmites* on the south side of the forest at a spot where there is a long and narrow channel of deeper water close to the south bank. This channel extends as far as the society of pure *Carex paludosa*.

It is possible that the inlet of the Boathouse Pool which divides the *Phragmites* zone into two masses, may be the remains of a channel which was

once continuous with the narrow channel along the south bank. On this interpretation, the community consists of two independent parts which fuse at their edges. There is an "island" community of *S. fragilis*, fringed with *S. cinerea* and *Phragmites*, and there is a "fan" community of *Alnus rotundifolia* and *S. fragilis* (see Map 5).

9. *The Great Rumex Marsh* (Maps 3 and 4).

The West Salix Marsh passes into a great expanse of *Rumex hydrolapathum* and *Equisetum limosum*, mixed with *Typha latifolia*. The region is 800 ft. long and 190 ft. wide, and is one of the largest regions in the marsh. Towards the southern bank there are three groups of *Carex paludosa* upon which are small forests of *Salix cinerea*. On the north side there are three narrow pools containing *Potamogeton natans*. Pure *Equisetum limosum* surrounds each pool. At the south end, the community is terminated by a society of *Phragmites*.

10. *The Phragmites Marsh* (Map 4).

At the south end of the marsh, the line of the deeper part of the old channel of the river moves over to the south side. The south end of the channel is almost filled with a society of *Phragmites*. The narrow channel pool which is left open on the south side is filled with *Nuphar*. There is another smaller society of *Phragmites* on the north bank opposite the end of the Great Rumex Marsh, and a third society on the south bank. *Equisetum limosum* is invading the channel pools and cutting them into sections.

11. *The South Salix Marsh* (Map 4).

The end of Butterby Marsh is occupied by a society of *Digraphis*, which is covered with a forest of *Salix fragilis*. In some places there is a mixture of *Digraphis* and *Phragmites*. *Carex distans* occurs under the trees, together with a few tufts of *Carex paniculata*. A little *Iris* and *Carex ampullacea* are found at the junction of the *Digraphis* and *Phragmites*.

III. THE ZONATION AND STRATIFICATION OF THE VEGETATION.

With few exceptions the plants of the marsh are uniformly distributed with reference to the water level. In the following table the principal species are shown in the observed order of their vertical distribution, as observed at various stations in the marsh. The number of species occurring in any one station varies from station to station, but there is no variation in the vertical sequence in which the species occur in the station.

The numbers giving the vertical range in inches of each species are approximate. The vertical range varies from species to species, and there is a good deal of overlapping where ranges are similar. The range of the species in the list from *Scirpus sylvaticus* to *Juncus communis* is small, and the vertical succession of the plants is difficult to fix accurately. *Rumex* and *Equisetum* have very considerable vertical ranges.

Table I.

	Vertical Range in inches above (+) and below (−) high-water mark (0)	Long Pool				Typha Marsh		East Salix Marsh	East Pasture			East Bay	Boathouse Pool		Alnus Forest	West Salix Marsh	Great Rumex Marsh
		West Shore	East Shore	Delta	South End	East Shore	C. pal. Island		Iris Marsh	Woodside Marsh	Middle Marsh		North Bay	West End of Boathouse Wood			
Deschampsia caespitosa	+ 6	.	.	.	.	.	.	×	.	×	.	.	×	.	.	.	.
Juncus glaucus	+ 6 0	.	×	×	.	×	.	.	×	×	×	×	×	.	.	.	.
Digraphis arundinacea	0 − 2	×	×	×	×	×	.	×	.	.	×	×	×	×	×	.	.
Scirpus sylvaticus	0 − 2	.	.	.	.	×	×	.	.	×	.	.	.	.	.	.	.
Carex paludosa	0 − 2	×	.	.	×	.	×	.	×	×	.	×	×	×	.	.	.
Caltha, Mentha, etc.	0 − 2	.	×	×	.	×	.	×	×	.	×	×	×	.	.	.	×
Juncus communis	− 1 − 3	.	×	.	.	×	.	.	×	.	.	×	.	.	.	.	.
Iris pseudacorus	− 3 − 6	.	×	.	.	×	.	×	×	.	×	×	×	×	×	.	×
Sparganium ramosum	− 4 − 9	×	×	×	.	×	.	×	.	.	×	.	×	×	.	.	×
Rumex hydrolapathum	− 2 − 18	×	×	×	.	×	×	×	×	×	.	×	×	×	×	.	×
Equisetum limosum	− 2 − 30	.	.	×	.	.	.	×	.	.	.	×	×	×	.	.	×
Nuphar luteum	− 30 − 90	×	×	×	.	.	.	.	.	.	.	×	×	×	.	.	.

The distribution of certain plants appears to be related to factors other than that of the water level:

(*a*) *Phragmites communis* occurs in societies which occupy the steeper banks of the channel where there is deep water close to the bank. The plants cover the bank from slightly above h.w.m. to a depth of 2 ft. 6 in. below h.w.m., where they are succeeded immediately by *Nuphar*. The societies are not part of the present dominant marsh vegetation, but are probably relics of the reed swamp association of the old river (see p. 126). The determining factor in the occurrence of *Phragmites* is probably the presence of a silty or sandy substratum (see Pearsall (7)), but this has not yet been demonstrated in the marsh.

(*b*) *Scirpus lacustris* is another member of the reed swamp association, but it does not occur in the marsh in sufficient abundance to determine its relationship to the rest of the marsh flora.

(*c*) *Typha latifolia* has a vertical range from a few inches below h.w.m. to about 2 ft., but it does not form definite zones among the other marsh vegetation. Its distribution seems to be determined partly by stagnation conditions. The only *society* of *Typha* occurs in the shallow saucer-like depression of the Typha Marsh, where the absence of free communication with the water of the Long Pool, or with the water channel on the west side of the island of *Carex paludosa*, brings about stagnation conditions. In the rest of the marsh, *Typha* occurs scattered about in the *Rumex-Equisetum* community. *Typha* does not occur at the south end of the East Salix Marsh, where there is a small pool, and where the drain from the Middle Marsh of the East Pasture runs in, nor

does it occur in the Iris Marsh, which is irrigated by the drain from the Woodside Marsh. It is found in the broad expanse of *Rumex-Equisetum* at the north end of the East Salix Marsh, and in the Great Rumex Marsh.

(*d*) *Juncus glaucus* shows a very marked zonal distribution but the zones occur only in pasture land and on low slopes, and the plant is absent from the

WEST SALIX MARSH   EAST SALIX MARSH
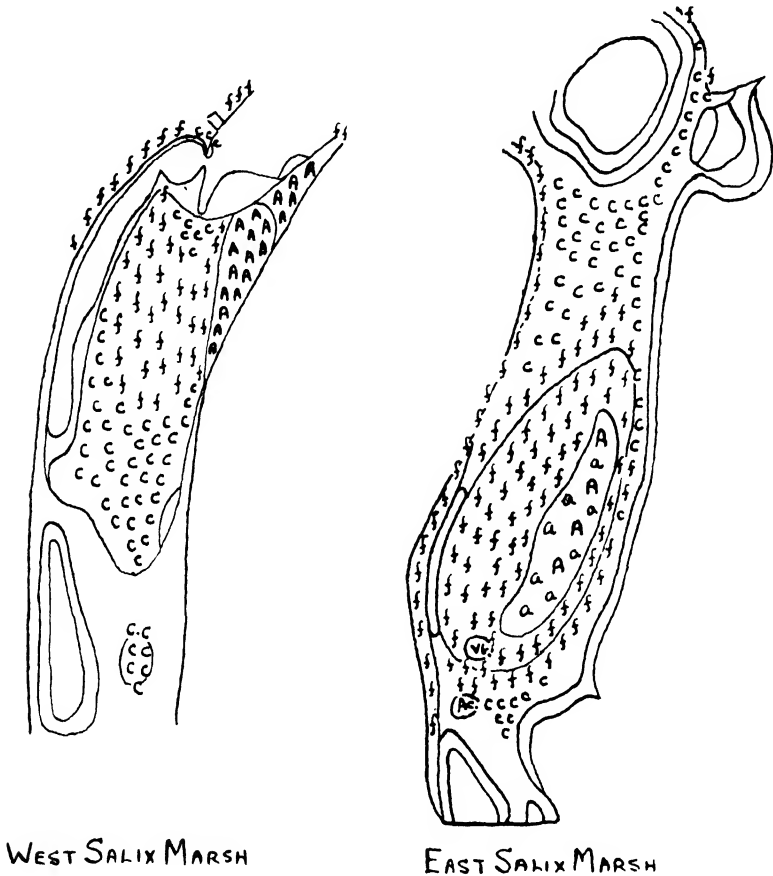
MAP 5. Marsh-forest vegetation of East and West Salix Marshes: herbaceous consociations shown only in outline. Symbols as in Map 2 inset, with addition of *Vb. Viburnum opulus, Ac. Acorus calamus*.

edge of the arable land and from the steep slope of the pasture field bank on the north side of the Great Rumex Marsh. It is possible that its distribution is affected by a biotic factor, namely the grazing of cattle, and the consolidation of the ground by the trampling of cattle and the passage of human beings.

Although observation shows that the majority of the plants of the marsh are distributed with reference to the water level, the explanation of the fact is not simple. The distribution is the result of many factors, of which the habit

and anatomy of the plant, and peculiarities of seed transport and seed germination, are some of the chief (see Arber (**1**); Guppy (**4**), pp. 37, 39, 85, 535).

The vertical range of each plant is delimited by the maximum and minimum water levels between which the conditions of the habitat are suitable for the plant. As each plant is of a certain bulk and occupies a certain vertical space and horizontal area, the occurrence of the plant depends not only upon the range itself but also upon the presence of an area of ground between the maximum and minimum water levels of the range sufficiently large to accommodate the plant. The size of the area depends upon the sine of the angle of slope of the shore. If the angle is small, the area between any two maximum and minimum water levels is large, and vice versa.

In the marsh the angles of slope, as determined by drawings made to scale, are as follows:

Above-water slopes: steep west bank of channel of marsh, 30°–40°; lower east bank of channel of marsh, 12°–15°.

Submerged slopes: Long Pool; steep east and west shores, 15°; at Delta, 7°; the ledge covered with *Rumex* on the north-east side of pool, 2°. Boathouse Pool; east and west shores of round reach, 6°–7°. East Salix Marsh; westward slope of *Deschampsia-Digraphis* island, 0° 30', eastward slope, 2°. Great Rumex Marsh; east to west, 2°.

With angles of slope of the order of one or two degrees, very small irregularities in the plane of the slope will considerably alter the area available for colonisation between any two water levels. The absence of the full number of members of the marsh association from various stations may be due to such irregularities, e.g. the absence of *Equisetum* from in front of *Rumex* on the north-east shore of the Long Pool; the absence of *Carex paludosa* from the East Salix Marsh consociation; the absence of *Deschampsia caespitosa* from the east shore of the marsh. Similarly, irregularities in the plane of a low slope may also lead to overlapping and mingling of plants of different zones, e.g. the confusion of zones in the cattle-trampled edge of the south end of the Typha Marsh (see p. 112); the mixture of *Rumex*, *Sparganium*, *Iris* and *Juncus communis* at the north end of the Typha Marsh; the mingling of *Carex paludosa*, *Rumex* and *Iris* in the West Salix Marsh.

The surface of the shore is not normally a plane, however. At the margin of the water the bank is always being more or less undercut by ripple action. The bank collapses, and the fallen material forms a narrow marginal slope of relatively steep pitch, but further out in the water the eroded material is spread out in a low submerged slope. The plants of the higher zone have a smaller area available for colonisation than those of the lower zones because the marginal slope tends to be relatively steep. It will be only rarely that by some peculiarity of topography there is a large area for the development of the plants of the upper zone. In the marsh, an area of this kind is probably to be seen in the *Digraphis* island in the East Salix Marsh, where there is a com-

munity of high-level plants extending over a great area. The community probably occupies a former bank of sediments which lay in mid-channel, and was exposed as the water level fell. The West Salix Marsh community probably occupies a similar bank.

The areas available for habitation by the lower-level plants are much more extensive, owing to the smaller angle of slope of the shore at lower levels. Communities of these plants, i.e. *Rumex, Equisetum, Iris*, etc. are the chief features of the vegetation of the marsh.

The stratification of the marsh forest vegetation is as follows:

Table II.

Locality	Trees	Ground vegetation
Typha Marsh (Carex paludosa Island)	Alnus, S. alba Salix fragilis	Carex paludosa, Scirpus sylvaticus C. paludosa, Rumex hydrolapathum
East Salix Marsh	Alnus, S. alba Salix fragilis Salix fragilis Salix cinerea	Deschampsia caespitosa Digraphis, Scirpus sylvaticus, Caltha Rumex, Equisetum, Iris, Sparganium Rumex, Equisetum, Iris, Typha
West Salix Marsh	Alnus Salix fragilis Salix cinerea	Digraphis, Carex paludosa Carex paludosa, Rumex, Iris Carex paludosa, Rumex, Iris, Equisetum
Great Rumex Marsh	Salix cinerea	Carex paludosa, Rumex, Iris, Equisetum
South Salix Marsh	Salix fragilis	Digraphis

The stratification of the plants of the upper-level zones of the marsh has not yet been investigated.

The stratification of the lower-level plants is as follows:

(a) On the surface: *Rumex hydrolapathum*. Near the upper limit of its range, the rhizomes are often covered with a dense carpet of mosses, viz. *Mnium affine* var. *elatum* and *Hypnum fluitans* var.

(b) Immediately beneath the surface: *Iris pseudacorus*.

(c) About an inch beneath surface: *Sparganium ramosum*.

(d) Two or three inches beneath: *Typha latifolia*.

(e) Six inches beneath: *Equisetum limosum*.

IV. THE DEVELOPMENT OF THE MARSH ASSOCIATION.

The fall in the water level of the original channel of the marsh was probably due to the erosion of the bed of the river in the new channel which was cut across the neck of the loop. The river was shortened by nearly a mile, and the resulting acceleration of the current brought about a vertical erosion of the bed for a considerable distance both up and down the course of the river. If the fall of the water level in the loop has been some 2 or 3 ft., then the highest parts of the present floor of the marsh, namely the East and West Salix Marshes, must have been from 1 ft. 6 in. to 2 ft. 6 in. under water. This depth of water would permit the growth of *Phragmites, Scirpus lacustris* and *Equisetum limosum* (and possibly *Typha* in stagnant places), but would exclude *Rumex, Sparganium, Iris* and the plants of the higher zone. It would also

exclude all the marsh-forest trees. The present flora of the Typha Marsh, and the East, West and South Salix Marshes would be replaced by *Phragmites, Sc. lacustris* and *Equisetum*, the last probably being the most abundant. The Great Rumex Marsh would be open water, and the Long Pool and Boathouse Pool would be longer, broader, and deeper. This reconstruction agrees with Surtees' description (see p. 105), and is also confirmed by the presence of fragments of *Equisetum* in the deposit of grey clay under the present Typha Marsh.

On these grounds it is probable that the societies of *Phragmites* represent original vegetation which is now in process of retrogression, but the *Rumex-Equisetum* community and the marsh forests, are secondary and have arisen by the colonisation of the channel from the littoral region (including the marshes of the East Pasture) as the water level fell. The colonisation phase is now over and the present phase is one of autogenous development of the habitat. The vegetation is making a new substratum out of autogenous products of decay, and the floor of the marsh is being raised and the relative position of the level of the h.w.m. is being changed. The accumulation is most marked in the *Rumex-Equisetum* community, where the bulky rhizomes of *Rumex* tend to grow on top of one another. A hole was dug in the south end of the *Rumex-Equisetum* community of the East Salix Marsh in the summer of 1929 when the water level was abnormally low, and the following stratification of deposits was found:

(*a*) Stratum about an inch thick, consisting of living rhizomes of *Rumex*, covered with, and embedded in, dense masses of *Mnium* and *Hypnum*.

(*b*) Stratum from 3 to 5 in. thick, consisting of three successive layers of old rhizomes of *Rumex*, embedded in finely divided black detritus. The old rhizomes were black, hard and semi-carbonised.

(*c*) Stratum 7 to 9 in. thick, consisting of dark coloured finely divided detritus, densely penetrated by living and dead rhizomes of *Equisetum limosum*.

(*d*) Basal stratum of clay silts.

The stratification indicates that at this particular spot there has been an accumulation of autochthonous detritus to the extent of about 1 ft. during the period of 100 years which has elapsed since the marsh was formed. The invasion of the *Rumex-Equisetum* community by *Salix fragilis* (pp. 115, 116) is probably a result of the increase in the height of the surface by autogenous accumulation.

Phot. 3. Boathouse Pool.

Phot. 4. Great Rumex Marsh.

Phot. 1. Long Pool.

Phot. 2. East Salix Marsh.

me a grant of £100 with which to erect and equip a small laboratory at the Long Pool and to purchase a boat for use on that piece of water. I am further obliged to Lt-Col. Salvin for allowing the laboratory to be erected and for providing material towards its erection. The hydrobiology of the pools is being worked simultaneously with the ecology of the marsh, and the results will be published in due course.

REFERENCES.

(1) **Arber, Agnes.** *Water Plants.* Cambridge, Univ. Press, 1920.
(2) **Baker** and **Tate.** "Flora of Northumberland and Durham." *Natural History Transactions of Northumberland and Durham*, 1867, **2**, 1868.
(3) **Greenwood, C.** *Map of County Palatine of Durham*, from actual survey made in the years 1818 and 1819 by C. Greenwood. London, 1820.
(4) **Guppy, H. B.** *Observations of a Naturalist in the Pacific*, **2**, 1906.
(5) **Hutchinson, W.** *History and Antiquities of the County Palatine of Durham*, **2**, Newcastle, 1787.
(6) **Ornsby, Rev. G.** *Sketches of Durham.* Durham, 1846.
(7) **Pearsall, W. H.** "Aquatic vegetation of the English lakes." This JOURNAL, **8**, Dec. 1920.
(8) **Surtees, R.** *History and Antiquities of the County Palatine of Durham*, **4**, 1840. City and Suburbs of Durham.
(9) **Winch, N. J.** "Flora of Northumberland and Durham." *Transactions of the Natural History Society of Northumberland, Durham and Newcastle-on-Tyne*, **2**, 1838.

DESCRIPTION OF PLATES XVII.

Photographs all taken in early summer, 1930.

Phot. 1. The Long Pool, northern half: taken from Delta on east bank, looking north. In foreground, *Juncus glaucus* zone, passing into zones of *Digraphis* (not well shown), *Rumex hydrolapathum*, and *Equisetum limosum* (concealed by *Rumex* zone). On left-hand bank of pool, *Phragmites*. In open water, *Nuphar*. In the distance northward, edge of *Rumex-Equisetum* community of the Typha Marsh.

Phot. 2. The East Salix Marsh, south end: taken from south-west corner of the triangular pool, looking north-east across the East Pasture to Croxdale Wood. In foreground, triangular pool with *Potamogeton natans*, and fringed with pure *Equisetum limosum*, passing into *Rumex hydrolapathum*. In background on the left, marsh forest of *Salix fragilis*, with some *S. alba* and *Alnus*, but the two latter are not distinguishable in photograph. In front, marsh forest of *Salix cinerea*, lying in the *Rumex-Equisetum* community.

Phot. 3. The Boathouse Pool, southern end (round reach): taken from east shore, looking west. The Long Reach of the Pool runs into the distance from right to left. In foreground, zone of *Juncus glaucus*, passing into zones of *Iris*, *Rumex-Equisetum*, pure *Equisetum*, *Nuphar*. Trees of *Salix cinerea* are seen on left and in middle foreground. The West Salix Forest is seen in far distance on the left. On the right is the Boathouse Wood.

Phot. 4. The Great Rumex Marsh: taken from north bank, looking south-west. The *Rumex-Equisetum* community occupies all the channel. The floating-leaved aquatic plant is *Pot. natans*. The lighter-coloured vegetation in the distance is *Phragmites*. The marsh-forest vegetation is *Salix cinerea*.

FISHERY RESEARCH: ITS CONTRIBUTION TO ECOLOGY

By E. S. RUSSELL, O.B.E., M.A., D.Sc., F.L.S.

(Director of Fishery Investigations, Ministry of Agriculture and Fisheries.)

INTRODUCTION.

IT is an unfortunate result of specialisation that the data obtained and the methods worked out in one branch of research may escape the notice of those engaged in similar work along different lines and with a different object. One striking instance of this is found in the study of animal behaviour, where the purely psychological literature on the subject is as a rule unknown to and unappreciated by the zoologist or the physiologist. Another example forms the subject matter of this paper.

From the point of view of a rational classification of the sciences fishery research is, by reason of its methods and standpoint, simply a branch of ecology. Its methods and results are, however, not well known among professional ecologists. The main reason for this is of course that the literature of fishery research is specialised, and is for the most part published in journals which the ecologist rarely sees. And if he wants to see them he has generally some difficulty in obtaining them. It is the special purpose of this paper to direct attention to some of the results of fishery work which have a particular bearing upon ecological problems, and to serve as an introduction and guide to the literature of fishery research, with special reference to the English work. Naturally it will not be possible to cover the whole field in detail—one can give only a bare outline of some of the aims and results of fishery work, and not a full review or summary. Nor do I propose to deal with general marine research, except in so far as it is directly utilised in the special fishery investigations with which I am mainly concerned. Such general marine biological work is of course much better known to the professional zoologist and botanist than the more specialised researches of the fishery worker.

I. ORGANISATION OF FISHERY RESEARCH IN N.W. EUROPE.

There are few maritime countries nowadays that do not engage in research for the benefit of their sea fisheries, but it may safely be claimed that the nations of north-west Europe led the way in oceanographical and fishery research.

The systematic study of the sea, which started in earnest about a hundred years ago, was carried out at first in connection with the work of survey and exploration undertaken by the naval ships particularly of Great Britain and

the United States. Also about a century ago zoologists began to extend their researches from the littoral zone out to deep water by means of the dredge. The tow-net was introduced in 1845, and 20 years later (in 1865) G. O. Sars made one of the fundamental discoveries in fishery research—that the eggs of the cod float freely in the water, and are therefore not directly affected by fishing operations. This was soon found to be true of the majority of food fishes. The period of the great oceanographical expeditions came later, initiated by the *Challenger* Expedition of 1872–6, and represented in recent years by the German *Meteor* Expedition, the Danish *Dana* Expeditions, and the elaborate study of whales and whaling undertaken by the British *Discovery* Committee in the Antarctic and South Atlantic with the ships *Discovery II* and *William Scoresby*. A convenient summary of the history of oceanographical research up to 1910 will be found in Murray and Hjort (1).

Fishery research gradually developed during the second half of last century, mainly in the Scandinavian countries, in Germany and in Great Britain, and mainly in connection with practical problems (see 2). Confronted with complaints that the sea was becoming depleted of fish, or that certain fisheries had inexplicably failed, the legislator turned to the marine zoologist for information and advice. Little was known fifty or sixty years ago about the life history of our common fish, and the need for elaborate and widespread investigation soon became evident. In this country fishery research was started in the 'eighties by the Fishery Board for Scotland, and not long afterwards the problems were taken up in England under the auspices of the Marine Biological Association, which in the early years of this century conducted fishery research on behalf of the Government.

At the beginning of the present century an important step was taken by the foundation of the International Council for the Exploration of the Sea, with headquarters at Copenhagen. This organisation, in which practically all the maritime nations of north-west Europe take an active interest, has had a great influence in stimulating research, in working out adequate and standard methods, and in co-ordinating the work of the participating countries. It had at its origin two main interests, the scientific investigation of the sea in all its aspects, and the study of the practical problems of the sea fisheries, especially the problems of "Overfishing" and "Fluctuations." Both interests are still fully represented in the present-day activities of the Council (see 3). The need for international co-operation in the study of the sea and in the study of fisheries is obvious. The sea and its problems are one; what happens in one little corner cannot be interpreted without reference to what is going on elsewhere; what happens in the North Sea, for instance, depends to a large extent upon the set of the currents, and they in their turn are linked up with the general circulation of waters in the Atlantic. The main fish stocks lie in international waters, and any proposal for the regulation of fisheries must gain international consent if it is to be effective. The Council's activities extend over all the

grounds fished by the participant nations, from the Barentz Sea and Bear Island in the north to the coast of Morocco in the south; and westwards as far as the Newfoundland Banks and the west coast of Greenland. Similar work is also being done by Canada and the United States, and is likely to extend in the near future, so that in effect all the great ocean-system of the North Atlantic is being kept under observation.

The actual means adopted for the collection of the vast mass of data required will be considered in the next section. Here only a few words as to the actual equipment for fishery research in this country may be added. The direct researches into the economic problems of the sea fisheries are carried out by two Government Departments, the Fishery Board for Scotland, and the Ministry of Agriculture and Fisheries (for England and Wales). Both have marine laboratories, at Aberdeen and Lowestoft respectively. Both keep in commission throughout the year a sea-going trawler fitted up for scientific work, and a large motor boat for investigations nearer shore. In addition to the more strictly fishery work, various marine laboratories round the coast, notably at Plymouth, Millport and Cullercoats, undertake general marine research, not specifically directed towards the solution of fishery problems, but aiming at the extension and refinement of our knowledge of the conditions of life in the sea. They are assisted from Government funds as playing an important part in the general investigation, and close co-operation exists between the official and the independent institutions.

II. Scope and methods of fishery research.

It is important to realise the vast extent of the area which is, or should be, covered by the fishery investigator. British fishing vessels range over an immense stretch of sea, from the edge of the ice barrier in the north right south to the coast of Morocco. The fisheries round Iceland are second in importance only to those of the North Sea, and of recent years the waters to the west of Greenland have been energetically exploited for halibut and cod. Fishing is confined on the whole to comparatively shallow waters, inside about 300 fathoms, and the bulk of the catch is taken in much shallower depths than this. The main reason for this restriction is that the food fishes are on the whole much more abundant in coastal waters, and the oceanic waters and the deep sea are not at present worth exploiting, even if gear suitable for the purpose existed. The great bulk of the bottom-living or demersal fish are taken by the trawl, which cannot in practice be used with effect beyond a certain depth. Fishing then is limited to the continental shelf, using this word in a loose sense to cover areas, mostly adjoining the land, which are of less depth than about 300 fathoms. It follows that there are definite limits to the extension of the possible fishing grounds. Forty or fifty years ago the North Sea was the main area fished, but as this became less profitable owing to the increase in the intensity of fishing, the vessels went farther afield, opening up the great

fishing grounds round Iceland, in the Barentz Sea, and all along the edge of the deep water off the western coasts of Europe. One is tempted to say that all the possible fishing grounds within reach have now been explored, but the amazing success during the last two or three years of the fishing near Bear Island gives one pause. Further exploratory and surveying work was to have been undertaken in northern waters by a new survey ship, but the need for national economy has led to postponement.

The fishing grounds being so vast and wide-spread, how is it possible to keep them under observation? This is done first of all by the research vessels of the various countries, which carry out regular cruises in the more important areas. But these vessels are few in number, and many regions can be visited only occasionally, if at all. Our English vessel confines her operations mainly to the southern half of the North Sea, with an annual cruise to the waters off the south and west of Ireland, for the purpose of studying the hake. The Scottish vessel takes the northern North Sea and the waters round Orkney and Shetland, with visits to the Faroes and Iceland and the west coast of Scotland. The research vessels of other countries are similarly restricted in range.

In addition to the specialised investigations of the stocks of fish, the bottom fauna, plankton and hydrography, carried out by means of research vessels, we have fortunately another source of information—the fishing vessels themselves. In a sense every deep sea fishing vessel is a research vessel, for each one provides, voluntarily, information as to the quantities and kinds of fish landed, classified roughly by sizes, where they were taken, what gear was used, the length of the voyage, and the number of hours actually spent in fishing. From such information, which is collected daily at all the main fishing ports in Great Britain, it is possible to form a very accurate idea of the yield of the fisheries, to relate the amount of fish landed with the fishing power expended, and to follow out any periodic or any general change in the abundance and the average size of the different species of fish. Fishery statistics, in the highly elaborated development they have reached in this country particularly, are the basis of fishery research. They enable us to keep a rough but continuous census of stocks, in respect of gross abundance (given in terms of weight) and, approximately, of size. General information as to size and changes in size is available because all the more important fish are sorted on board and at the ports of landing into size categories, shown in our statistics as Large, Medium and Small, and from the changes in the proportion of these categories valuable deductions can be drawn as to the changes in the composition of the shoals, due to influx of young stock, the effect of intensive fishing, migrations, and so on.

In addition, the catches are in the main accurately located in space. It is now possible to allot the bulk of the landings of demersal fish to the particular rectangles in which they were caught, the rectangles being 1° east

to west and $\frac{1}{2}$° north to south. Such detailed data give a very good picture of the general distribution of each species in every month of the year, and enable us to follow its migrations, distinguishing in many cases the movements of the larger fish for spawning and the movements of the whole population for feeding.

An account of the methods used in collecting and working up fishery statistics will be found in (4) and (5).

Supplementing the general information obtained from the commercial statistics, more specialised data as to the size-composition of the catches are collected by a special staff, working partly on fishing vessels at sea and partly on the big coastal markets. At sea, large samples of the catch are measured regularly, including samples of the small fish which are discarded as of no commercial value; on the market, samples of the trade categories are similarly dealt with, and collections of scales and otoliths for age-determination made periodically.

Before the war, this work was carried out exclusively on the markets (see, for example, **6**); immediately after the war, the extremely interesting effects of the war-time restrictions on fishing were investigated by means of the observations of a staff of measurers working constantly at sea (see **7** and **8**). Nowadays both methods are employed. The scope of the fish-measuring work may be gauged from the fact that in 1929 fish to the number of 914,000 were measured at sea, and 69,500 on the markets.

Closely connected with the statistical investigation of the landings is the study of the age-composition of the stocks, which is energetically pursued in England in the case of plaice, cod, and herring, and in Scotland in haddock and herring. Particularly for haddock, plaice, and herring, what is aimed at is a regular census of the stocks in terms of year-groups, the age of the fish being read from the otolith (plaice) or the scale (haddock and herring). Nearly 20,000 plaice otoliths were examined by the English staff in 1929. The aims and results of this census work will be considered in more detail later.

Returning now to the work of the research vessels and other cognate investigations, one may say broadly that the aim is to study (1) the fish themselves, by collecting data as to their distribution, size, age-composition and migrations, their spawning places, their eggs and larvae and the drift of the same, and (2) all the environmental conditions affecting the fish, for example the amount and distribution of their food, whether found on the bottom or floating free in the sea as plankton, the normal set and variations in the currents which distribute their eggs and larvae and their planktonic food. In addition, experimental work is carried out with different types of fishing gear, with the special object of discovering a practical method of obviating the destruction of undersized fish. This line of work is now bearing fruit, for it is established that a moderate increase in the mesh of the cod-end or bag of the trawl would spare considerable quantities of the "round" fish,

such as haddock and whiting, which are now destroyed. The study of the food of fishes entails extensive examination of stomach contents—a report just issued (9) deals with the analysis of the stomach contents of nearly 14,000 herring—the quantitative investigation of the bottom fauna by means of the Petersen grab and other instruments, and of the plankton population by means of the elaborate modern technique. The study of migrations is carried out mainly by means of marking fish, such as plaice and cod, with two little vulcanite studs held together by silver wire. For example, about 2500 plaice were marked by the English staff off the Dutch and Danish coast in 1929, of which about 40 per cent. were recaptured by fishing vessels in the course of a year.

Hydrographical investigations, designed primarily, so far as the English work is concerned, to map out the current-system of the North Sea and English Channel, are effected partly by means of cruises of the research vessels and partly by continuous series of observations on Lightships and on steamship routes. Three main methods are used—the collection of regular samples for the determination of temperature and salinity, direct measurement of residual currents by means of the Carruthers drift indicator (10)—one has been in continuous use on the Varne Lightship in the Straits of Dover now for five years—and by the employment of drift bottles, designed to float on or near the surface or to trail along the bottom, and in some cases to float for a deter-mined period and then sink and anchor themselves.

It will be seen from this cursory review of the methods of fishery research that the investigations are wide in character, and trench on the province of several sciences. They can be tackled only by team work. Furthermore, the problems are all of long range and require many years of continuous observa-tion for their approximate solution. The need for continuity is especially obvious in fishery statistics and in the running census of size and age which is kept up for the main species of fish. Only by long years of work is it possible to assess the true meaning of changes in the stock of fish, and to distinguish more or less regular and periodic fluctuations from any general trend due to fishing operations or other causes.

From the point of view of ecology, the work is of interest also in that it entails a very thorough and comprehensive study of the life-history and life-conditions of single species of fish—autecology on a big scale. It has been said that more is known about the general life-history of the plaice in relation to environment than about any other species. This may or may not be so, but it is certainly true that the data collected about the main species of fish are on a scale not easily paralleled in zoological research, apart from some other branches of applied research.

III. The census of fish populations and its aims.

It is in a sense misleading to speak of an actual census of fish populations, for no attempt is as a rule made to estimate the absolute numbers of any species existing in a given area; we content ourselves with comparative values, which are quite sufficient to show the broad changes in abundance. Certain absolute figures are fairly accurately known, for instance the actual total quantity caught. In certain species the rate of mortality can be estimated with some degree of accuracy, and it would be possible to form a pretty good estimate of the actual weight or numbers of the stock existing in an area at a particular time. In practice however it is easier to work with measures of relative abundance, such as the landing per hundred hours' fishing, and indices of this kind give us in effect all that we want.

It is known with certainty that one of the main factors affecting the quantity and the size-distribution of the stock is the intensity of fishing. Direct evidence of this is afforded in some species by marking experiments. Thus it is definitely known in the plaice that up to 50 per cent. or more of the marked fish may be recaptured in a year by fishing vessels. As a rule the recapture rate is not so high as 50 per cent., and it varies considerably, in accordance with the local intensity of fishing and also with the effectiveness of the marking. But it amounts generally to a very substantial percentage, giving a minimum figure for the effect of fishing operations on the stock. The figure is a minimum one, for not all the recaptured marked fish are reported, a proportion of the marks may work out and be lost, and of course some of the marked fish may die.

In herring, which have never been successfully marked, indirect methods of calculation have indicated mortality rates in the commercial stock of 20 per cent. per annum in the Norwegian spring fishery and 50 per cent. or more per annum in the East Anglian fishery (see **11** and **12**).

Clear indications of the effect of fishing upon the stocks of fish can also be obtained from the general statistics, particularly from the changes in the landing per unit time, though such changes are also markedly affected by the large-scale fluctuations in abundance, due to natural causes, which occur in most species (see next section). The war provided a striking object-lesson on the influence of fishing upon the abundance of the stock. Fishing operations were naturally very much restricted during these years—the English landings of bottom fish fell in 1917 to rather less than 30 per cent. of their normal amount—with the result that the mortality rate due to fishing was materially decreased. More fish survived, stocks were gradually built up, so that in 1919 and 1920, when fishing was again actively prosecuted, landings were considerably higher, and the average size of the fish was somewhat greater. Thus in the North Sea the average landing per day's absence by British steam trawlers rose to 31·1 cwts. in 1919 and 25·4 cwts. in 1920, as compared with 17·3 cwts.

in 1913. The increased yield did not however last very long, and the very intensive fishing of the years immediately after the war quickly wiped out the accumulation of the war years, with the result that the landing per unit time fell to approximately the pre-war level. The effects of the partial protection afforded by the war on the stock of plaice in the North Sea were very thoroughly investigated (see **7** and **8**) and yielded results of great significance. It was found that by the end of the war the plaice stock had reverted some way towards the state characteristic of an unfished or virgin ground. When the Barentz Sea grounds were first fished for plaice in the early years of this century, catches were very high, and they consisted of large old fish in rather poor condition. These represented the accumulation of years. As time went on these old fish were eliminated; the average catch decreased, and so did the average size of the fish, but their quality and their rate of growth improved, and more room was left for the upgrowth of new stock. In the North Sea during the war, plaice stocks began to accumulate, the average size of the fish began to go up, and growth-rate began to fall.

These observations emphasize the extreme complexity of the problem of "overfishing." Intensive exploitation of the stocks is not necessarily detrimental; it has on the contrary certain definite merits. It clears out the old slowly growing fish, gives opportunity for increased growth of the rest, and leaves room for the oncoming new broods. It can of course go too far, and lead to an extreme reduction in the numbers of the larger fish, only partially compensated for by their rapid growth and fine condition. This appears actually to have happened in the Belts and western Baltic (see **13**), where stringent measures of protection have become necessary for the plaice and flounder. A full discussion of the problem of the "rational exploitation" of the fisheries—by which we mean getting the highest annual yield compatible with a maintenance of the supply—would be out of place here (see however **14**), but the interesting point for our present purpose is that the problem can be adequately treated, as Petersen, Kyle and Garstang have always maintained, only from a comprehensive ecological and physiological point of view. Food supply is probably a critical factor. The best yield is presumably not to be got from a badly overcrowded population, where a large proportion of the available food is used for mere maintenance and little is available for growth (see **64**). The effective thinning out of the marketable stock brought about by fishing is undoubtedly all to the good, *provided it does not go too far*. It is all a matter of degree.

A very important practical question arises in this connection. There takes place at present a considerable destruction of undersized fish of little or no marketable value. Most of these if spared would in a short time grow to marketable size. Should we increase the yield of marketable fish if this were done? Commonsense says yes—and rightly. But the problem is not so simple as it seems, and the question of degree again comes in. Possibly

thinning at a very early stage might be advantageous, while thinning later on would be detrimental. Actually the problem is to some extent susceptible of exact mathematical treatment if we know certain fundamental food ratios, namely the amount of food relative to body weight required to keep weight constant, and secondly the relation between growth in weight and the amount of food required to produce this growth. Here fishery research requires help from physiology. Recently data of the kind required have been provided for the plaice by experimental work carried out by the Marine Biological Association at the instance of the Fisheries Department (see **15**).

While one of the main objects of the census of stocks in respect of abundance, size and age is to establish the effect of fishing operations, and of changes in the intensity of fishing, there is another problem involved which is of great importance both theoretically and practically, and that is the problem of fluctuations. But this requires a Section to itself.

IV. FLUCTUATIONS AND PREDICTION.

In his most interesting book, *Animal Ecology* (1927), Mr Elton remarks that the study of animal numbers constitutes about half of animal ecology, and he gives a fascinating account of what is known about the variations in abundance of land animals. We find the same phenomenon of big-scale fluctuations in marine animals, and ever since Hjort's paper of 1914 (**16**) the problem of fluctuations in the main species of fish has received much attention from fishery workers and has been very actively studied (see **17** and **18**).

The problem is anything but an academic one. In certain communities, notably in northern Norway, where the population is mainly dependent upon fishing for a livelihood, the success or failure of the fishing is, or used to be, almost a matter of life or death. It is natural, therefore, that the study of fluctuations was tackled first and most energetically in Norway. Under the guidance and inspiration of Dr Johan Hjort, then Director of Fisheries, aided by able assistants like Einar Lea and Oscar Sund, a vigorous attack was made upon the practical problem of why the great cod and herring fisheries showed such big variations from year to year. It had been thought by many that the fluctuations might be due to mass migrations, the fish coming in to their accustomed grounds in some years and not in others. The Norwegian investigations showed that this explanation was quite inadequate, and disclosed another, hitherto unsuspected, cause for the fluctuations. It happened, fortunately, that at the time Hjort's work started (in 1901) the technique of age-determination in fish by means of scales and otoliths was just being worked out. This method was applied with great success to the study of the herring, and it soon became established that the main cause of the fluctuations in the great spring herring fishery was the success or failure of the individual broods or year-classes composing the stock. Thus it was found that the 1904 year-class was remarkably abundant, and it predominated in the catches for

many years, providing a rich fishery. It still persisted, though in greatly reduced numbers, for some years after the war, and meanwhile the stock was replenished by other good year-classes such as those of 1913 and 1918; intermediate year-classes were very poor.

Similar methods applied to the Norwegian cod, supplemented by extensive measurements, demonstrated the existence of specially prolific brood-years, as for example those of 1904 and 1912, while other years contributed little to the stock.

The same general method of determining the age-composition of the stock, and particularly the abundance of the incoming year-classes or recruit-stock, has been used with success also in the North Sea, particularly by Dr Harold Thompson for the haddock and by Dr Hodgson for the East Anglian herring fishery.

Clear indications of big fluctuations in the haddock stock in the North Sea were noted by several workers before the war; there was, for example, quite definite statistical evidence that the year-class 1904 was very rich (see **19** and **20**).

After the war, under the direction of Dr Bowman, Scientific Superintendent to the Fishery Board of Scotland, who had paid much attention to the question, Dr Harold Thompson (**21**) made great advances in the study of these fluctuations in haddock, by the skilful application of the scale method of age-determination, coupled with the use of measurements and commercial statistics. He showed conclusively that in certain years, notably 1920, 1923, 1926 and 1928, the supply of haddock brood was very much above the average, while in the intervening years the supply was moderate or poor. A specially good brood-year may contribute to the stock up to 25 times as many young haddock as a poor year.

Obviously these big fluctuations in the supply of young stock must have a very great effect upon the success of the fishery in the ensuing years. This effect is first seen in rather less than two years in the haddock and persists for about two years; the intensive fishing to which the stock is subjected soon uses up even the best recruit-class. Thus the good brood-years of 1904 and 1923 were followed by high catches in 1906–7 and 1925–6 respectively. It is now possible from a study of the abundance and distribution of the youngest haddock (under one year old) to forecast with considerable accuracy the probable yield of the fishery in the North Sea during the next two years, and arrangements have been made at the instance of the International Council for the Aberdeen laboratory to prepare such forecasts. It is hoped that the English department will soon be in a position to predict in a general way the future of the cod fishery in the North Sea, basing the predictions on the study of the smallest market category of cod landed at Grimsby market (Graham, unpublished work).

In the case of the great East Anglian herring fishery, the biggest fishery

in the country, the continuous study for a number of years of the age-composition of the catches has made it possible to predict in advance the probable yield of the fishery, particularly as regards number and size (see **12**). For the last three years (1929–1931) experimental forecasts were published in the trade press before the season started, and these excited considerable interest and turned out to be in the main accurate (see **22**).

Little is known so far about the causes of fluctuations. One thing appears reasonably certain—that there is no necessary connection between the number of eggs produced in a particular spawning season and the amount of fry which survives; on the contrary, good brood-years have often been poor spawning years. The fate of the year-class is probably settled at a somewhat later stage, possibly in the larval or post-larval stage. Various factors have been adduced as probably affecting survival—lack of planktonic food for the newly-hatched larvae, variation in temperature, variation in the normal course of the currents drifting the larvae to localities unsuited to their growth and development. Much work still remains to be done before this complex problem can be elucidated. Clearly the problem is an ecological one, and nothing short of a full knowledge of the conditions of existence of the species concerned, of its relations to other forms of life, of its food and its competitors, will suffice to solve it.

An interesting case of fluctuations in catch, which can be accounted for by variation in hydrographical conditions, is reported by the late Dr A. C. Johansen (**23**) and by Jensen (**24**). Reference may also be made to the well-known work of Otto Pettersson (summarised in **25**).

The subject of fluctuations in fish-populations is a vast one and I have treated it only in outline. It has of recent years been very actively discussed by the workers of the International Council, and the reader who is interested may be referred for further details to the full discussions which took place at the meetings of 1929 and 1930 (see **18**).

The phenomenon of fluctuations is by no means confined to the fish, but is shown also by the fauna of the sea bottom. This became evident from the work of the Danish investigators, C. G. J. Petersen, H. Blegvad and P. Boysen-Jensen, to which fuller reference is made in section VI (see especially **62**). A specially striking case was discovered by Davis (**26**) on the Dogger Bank in the course of extended surveys of the fauna by means of the Petersen bottom-sampler or grab. He found that certain small bivalves, notably *Spisula subtruncata* and *Mactra stultorum*, occurred in some years in enormous patches or beds on this famous fishing ground, providing rich feeding for haddock and plaice. So thickly were they present, and so evenly distributed by sizes that it was possible to map out the extent of the patches, to contour them according to the numbers per square metre, and to estimate with considerable accuracy the total numbers present. Some of the beds covered an area up to 600–700 square miles, and contained "astronomical" numbers

of individuals—one bed of young *Spisula* for example had a population estimated at the prodigious figure of 4,500,000,000,000. It was specially noteworthy that these beds were composed, with only two small exceptions, of shellfish of one year-group only. Investigations continued over several years demonstrated that enormous changes took place from year to year in the extent and location of these beds, and hence in the stock of *Spisula* and *Mactra* on the Bank as a whole. Thus in 1922 vast quantities of young *Spisula* were present on the Bank, while in 1923 and 1924 the spat-fall was negligible and young *Spisula* almost absent. Davis considers that the most probable cause of these fluctuations is variation in the course of the currents by which the larvae are passively transported. The species are restricted to a particular type of bottom, and if they do not happen to be deposited by the currents on suitable ground the spat are wiped out.

Ecologists will find much of interest in these two papers of Davis, which show how much can be got out of a systematic and oft-repeated survey of a suitably chosen area of the sea bottom. His findings as to the relation between different species and the soil they inhabit are further referred to in Section VI. Confirmatory evidence of fluctuations in *Spisula* has recently been published by Hagmeier (**27**), and the extensive quantitative work on bottom fauna carried out since the war by other English, Scottish and German investigators has shown that fluctuations are the rule rather than the exception, and that this holds good also in the littoral region.

V. Distribution and migrations of fish in relation to environmental factors.

The study of the sea itself, particularly of its salinity, its temperature and its currents, has always played an important part in fishery research, and I can perhaps best indicate the bearing of this hydrographical work by treating it in direct connection with the problems centering round the distribution, dispersal and migrations of fish.

First as to geographical distribution—it is of course well known that the main species of food fishes are definitely restricted in their range, presumably by environmental factors such as temperature. Every fisherman knows that his fish have their times and their seasons, that they must be sought for on certain grounds, that they are not distributed evenly over the sea. He knows where to go for the kinds of fish he wants.

There is, for instance, a broad distinction between "northern" fish and "southern" fish. The cod is definitely a northern fish, being most abundant in the waters north and west of Norway, round Iceland, and on the Newfoundland Banks, still numerous in the North Sea as far as its middle portion, but rapidly decreasing to the south. The hake, on the other hand, is a southern fish, frequenting the warmer waters of the Atlantic slope, and fished for all the way from Morocco as far north as the Wyville Thomson Ridge between Shetland

and Faroe, but scarce in the North Sea. In the same way the herring is a northern species, being scarce south of the English Channel, while the sardine or pilchard is a southern form, extending from the Channel southwards and occurring, like the hake, in the Mediterranean.

Inside their total area of distribution, it is found that most fish form smaller geographical groups, spawning in particular areas, from which their eggs are distributed by the currents, and returning again to the same areas to spawn. Thus the cod of the North Sea, of the Norwegian coast, of Iceland, are separate stocks, each with its own spawning grounds and areas of distribution. Take for example the Norwegian cod. There is an enormous spawning concentration in spring about the latitude of the Lofoten Islands; the young are carried in the main north and east by the current which flows up the coast of Norway, many of them reaching the Barentz Sea, where they spend the first few years of their life. Many of the big fish, after they have spawned, also migrate hundreds of miles to the north and east, to return next year to the same spawning grounds. So, too, in Iceland, spawning takes place in spring in the warmer waters to the south and west of the island, from which area the fry are drifted round to the north and east coasts. The great majority of the plaice in the North Sea collect for spawning in a particular area off the estuary of the Thames in winter, where a tongue of warmish water extends up from the Channel, and their eggs and larvae are drifted to the north and east by the prevailing current, to reach the shallow Continental flats where they find suitable conditions for their further development (see **28**).

In general one may say that the life-history and migrations of a fish-group— I purposely avoid the controversial word "race"—take place within a closed circle; as a rule the fish move up-stream to spawn and their eggs and larvae are distributed downstream by the currents; spawning areas and feeding areas are often distinct and may be widely separated, and migrations are mainly for the two purposes of feeding and spawning.

A most elaborate and interesting account of the spawning places and areas of distribution of the fry of the Gadoids will be found in the papers of Damas and Johannes Schmidt (**29**), where it is shown that the numerous species inhabiting the European side of the North Atlantic have each their clearly defined spawning places, whose limits are closely related to hydrographical conditions such as temperature, salinity and currents.

From this slight sketch it will be obvious that the study of hydrography, and particularly of the currents, is fundamental for an understanding of the life of the fish, and may throw great light upon the causes of fluctuations.

As an example of the correlation which can be established between hydrographical and biological results we may take the work of Graham and Carruthers (**30**). After the main spawning areas in the North Sea had been mapped out by Graham (**31**) it became of interest to discover the subsequent distribution of the larvae and young fish. Basing his predictions upon a knowledge

of the prevailing winds and on drift-bottle experiments, Carruthers worked out the probable course of dispersal of the baby cod. Concurrent fishing experiments with special gear were made at intervals for the purpose of catching the larvae and the tiny fish, and good agreement was found between the estimated and the actual positions of the bulk of the pelagic fry during several months after the spawning season.

The methods used in the study of currents were briefly alluded to in Section I. They may be divided into direct and indirect. In the first category falls the use of drift bottles, and of the Carruthers drift indicator which measures direction and speed of resultant current (**10**). The continuous observations made with this instrument on the Varne Light Vessel in the Straits of Dover (see **32**) enable us to measure the amount of water passing from the Channel to the North Sea, to establish the variation in the flow according to the prevailing winds, and will it is hoped throw much light upon the fluctuations in the year-broods of plaice and herring which spawn in the vicinity. Drift bottles, particularly surface bottles and bottom trailers, were employed on a very big scale in the southern North Sea shortly after the war in connection with the intensive plaice investigations, and yielded a good picture of the circulation of the water in this area at different seasons of the year (see **33**). Smaller experiments are often carried out for specific purposes, as for example to trace the probable distribution of fish-eggs and fry from a particular locality, and a good deal of work on a larger scale has been done in the English Channel with bottles of different types. As might be expected a close relation exists between wind and surface drift, and the Channel work has enabled this to be precisely formulated (see **34**). In the northern part of the North Sea extensive drift-bottle experiments have been carried out by the Fishery Board for Scotland (see **35**). For a description of the different types of drift bottle in use reference may be made to (**36**).

The general course of the currents may be worked out also by indirect methods, particularly by the study of salinity distribution. If a sufficient number of regular observations of salinity are made it is possible to draw the isohalines for different times of the year, and from their general shape and inflections to infer the general movement of the water. It is an important part of the work of the International Council to organise such systematic sampling, principally from steamships plying on regular routes and from Light Vessels, though much information is also collected during the cruises of research ships. The tabulated results, mainly temperature and salinity, are published annually in the *Bulletin Hydrographique*. England is responsible for this work in the English Channel, and also for several steamship routes across the North Sea and North Atlantic. The collection of water-samples from steamships has been greatly facilitated by the special surface sampler invented by Lumby, which can be used from very fast ships (see **37**). A preliminary study of the results obtained in the English Channel will be

found in (**38**); for the general deduction of currents from salinity distributions in the North Sea reference may be made to the paper by Böhnecke (**39**).

That the direct and the indirect methods of working out currents give results in harmony with one another is indicated by an interesting experiment carried out a year or two ago in the southern half of the North Sea (see **40**). With the assistance of the Naval Fishery Patrol a rapid survey was made of a large area of the sea, which enabled detailed charts of salinity distribution to be prepared. At the same time direct current observations were made from the research vessel by means of the drift indicator at critical points. Good agreement was found between the general circulation deduced from the salinity charts and the actual currents shown at the selected points.

The study of temperature is also of direct importance, so much so that in certain areas, like the Barentz Sea, the Newfoundland Banks, and the cod spawning grounds off the Norwegian coast, the use of a thermometer is of great assistance to the fishermen in finding the fish. It has been established, for instance, that the spawning cod on the Norwegian coast frequent principally water between 4° C. and 6° C. (see **40 a**). In the Barentz Sea the chief fish, cod, haddock and plaice, are found in the warmer waters coming under the influence of the Atlantic stream and are absent in the cold waters flowing down through the eastern part of the area from the Arctic seas; they definitely avoid water below 0° C., which is fatal to them.

In the North Sea itself there is a curious discontinuity of distribution affecting both fish and bottom fauna, which is no doubt connected with the fact that in the northern half, roughly north of the Dogger Bank, there is for a considerable part of the year a colder bottom layer of water, marked off from the upper warmer layer by a definite thermocline. South of this area the water is more or less homogeneous in respect of temperature and salinity. Just where the two areas meet between the Dogger Bank and the English coast there is a rather definite change in the fauna; thus the common dab is replaced to the north by the long rough dab, and certain gadoids appear which are scarce or absent in the south. No systematic study of this transition area has yet been made, but it will be undertaken as soon as opportunity offers. The influence of temperature upon rate of growth is well known, and in haddock, cod and plaice rate of growth can be correlated to some extent with the temperature conditions of the areas in which they are found.

A striking demonstration of the effect of temperature conditions upon the life and movements of fish was afforded by the abnormally cold weather of the early months of 1929. Quite a number of bottom-living fish were killed in the eastern part of the North Sea by the excessive cold, and some species, particularly soles, showed an unusual migration outwards towards deeper water, no doubt in an effort to escape from the icy cold of the Continental flats where the effect of the severe winter was especially marked (see **41**).

The study of the plankton also throws considerable light upon the move-

ments of the fish. In the early days of the International Council's investigations, plankton and hydrography were studied together by means of systematic quarterly cruises, and a great deal of valuable information was obtained showing the general relation between the character of the plankton and the source of the water containing it (see **42**). Thus the degree of influx of the high salinity Atlantic water into the Channel and the North Sea could be gauged to some extent by the distribution of characteristic planktonic forms. Nowadays, when .the general distribution and seasonal changes in the plankton populations are known in their broad lines, interest has shifted rather to the study of the plankton in its direct relation to the fish. All larval fish, and some adult fish, notably the herring, feed on plankton, and it becomes of importance from the fishery point of view to study the supply of planktonic food, its geographical distribution and its variations in amount and kind from season to season and from year to year. This aspect of plankton research will be considered in more detail in the next Section; here it will be convenient to mention another way in which plankton, particularly phytoplankton, appears to affect the movements of fish. It was suggested by Pearcey many years ago (1885) that the occurrence of dense masses of *Rhizosolenia* in the water might impede and divert the movements of herring shoals; it is common knowledge among fishermen that herring and mackerel seem to avoid "weedy" or "stinking" water, or water containing "baccy juice," all of which names are applied to water thick with vegetable or flagellate plankton, like *Rhizosolenia* and *Phaeocystis*. The question has been studied in the North Sea in relation to the herring by Hardy (**43**) and Savage (**44**), and evidence is accumulating that the normal concentration of the herring shoals which give rise to the big fisheries may be seriously affected by the occurrence of great masses, particularly of *Phaeocystis*, which may act as barriers disturbing and deflecting the normal movements of the shoals. By means of an ingenious torpedo-shaped instrument which can be towed behind a ship and collects plankton on a disc of silk, Hardy investigated the relation between the catch of herring and the plankton *in situ*, in the hope that the indications given by the plankton might be definite enough to be used as a guide by the fishermen in shooting their nets. The results were promising though not conclusive, and a further concerted attack upon the problem is being undertaken. From his original torpedo Hardy has developed a larger Continuous Plankton Recorder (see **45**), which was used with success on the *Discovery*, and in an improved form is now being employed in a large scale investigation in the North Sea, undertaken by Hardy's Department at University College, Hull, in connection with detailed studies undertaken by the Ministry. It is hoped that by means of this co-operation much light will be thrown on the general movements of plankton in the North Sea, particularly of organisms like *Phaeocystis*, and on the particular conditions that determine where and when the herring shoals will concentrate.

Of considerable practical importance also is the study of the diurnal up and down movements of plankton and other pelagic organisms. Especially in the case of herring and hake, the catches show a definite diurnal periodicity, which is to some extent correlated with the vertical movements of the organisms on which they feed (see **46** and **47**).

One great field of research in connection with the movements and migrations of fish has so far been little worked, namely the study of the behaviour of the fish. Obviously for an understanding of any ecological complex a knowledge of the behaviour of its animate components is fundamental; the study of behaviour and the study of ecology must go hand in hand. But it is not easy to study the behaviour of marine fish in anything like natural conditions, and little light has so far been shed on the question as to how fishes are guided in their feeding and spawning migrations. A good beginning has however been made by Bull, using the conditioned reflex method of investigation (see **48**), and some promising results (see **48** a) have been obtained by Graham from a practical study at sea of the behaviour of the herring vis-à-vis the net.·

VI. FOOD CHAINS AND ANIMAL COMMUNITIES.

I mentioned above that the plankton work undertaken in connection with fishery research is nowadays largely devoted to a study of the planktonic organisms that are of direct importance as food for fish. Much attention for example has been given to the food of the herring, which has been elaborately studied of recent years, especially by Lebour (**49**), Hardy (**50**), Jespersen (**51**), and Savage (**9**). Except in its very early stages, when it takes diatoms and peridineans, the herring feeds mainly upon zooplankton (chiefly copepods) and young sand-eels. The zooplankton is in its turn dependent on the phytoplankton, and this upon sunlight and the nutritive salts contained in the seawater. That is, of course, not the whole story, for there are intricate food relationships existing between the members of this great plankton community. Thus the medusae and ctenophores feed actively on copepods and on the herring larvae themselves, as was demonstrated by Lebour (**52**). Hardy has given a pictorial representation of this pelagic web of life, in relation to the herring and the organisms on which it feeds (**50**, Fig. 11), which illustrates clearly how complex are the ecological relations involved.

The cardinal importance of phytoplankton as an essential link in the chain of food production in the sea is of course a commonplace, and needs no emphasis here. But a word or two may be said about the very intensive researches which have been carried out during the last decade on the conditions of plant production in the sea, particularly by Atkins in this country and by Gran in Norway. Following up the pioneer work of Brandt, Raben, Nathanson, Matthews and others, and utilising new and improved methods, Atkins (**53**) has studied the phosphate, silicate, nitrite and nitrate contents of sea-water

from the English Channel and other areas, their seasonal variation, their variation with depth, their sources of replenishment, and the part they play as factors of plant growth. Phosphate appears to be a limiting factor, at least at certain times. Investigations of this kind have been taken up vigorously in many oceans, especially on the *Meteor* and the *Discovery* expeditions, and now form an essential part of all general marine investigations.

Gaarder and Gran (54) made an elaborate experimental study of the growth of marine plankton diatoms in relation to nitrogen and phosphorus compounds, and work of this kind has since been pursued by many workers, among whom may be mentioned Schreiber (55) and Marshall and Orr (56). Extensive researches, bearing on the same general problem, have been carried out by Poole and Atkins and others on the penetration of light in the sea (see 53 and 57).

The whole subject is so big and is developing so rapidly that it is quite impossible to give any adequate account of it here; I shall content myself with giving a few leading references (58), by means of which the reader will be able to orientate himself in the literature. The direct importance of these researches in relation to fishery problems lies chiefly in the light they may throw upon the causes of fluctuations.

Not only is the food-chain of pelagic fish and of fish-larvae thus pursued down to its ultimate elements, but similar researches are also being carried out on the nutritive relations of demersal or bottom-living fish. The investigation of the food of these fish has been for long an integral part of fishery research, and our knowledge of the subject is now reasonably complete. Careful studies have also been made of the distribution and abundance of these food organisms, and upon *their* food and feeding habits (see, e.g., Blegvad (59)).

In this field the pioneer work of the late C. G. Joh. Petersen was fundamental, and has provided the stimulus and inspiration for much subsequent research. It was done on a broad ecological basis, and owed much of its success and interest to this fact. Petersen's primary aim in carrying out his investigations was to determine the amount of fish food present in Danish waters. For this purpose he invented an instrument, the bottom-sampler or grab, which would bring up the soil and the animals contained therein from a definite area of the bottom, either $\frac{1}{10}$th of a square metre or $\frac{1}{5}$th. This instrument in its perfected state works very well on sandy or muddy bottoms and is in regular use in fishery work, though it has of course its limitations. Petersen found that his problem was no simple one, by reason of the fact that the character of the fauna varied very much according to locality, as well as exhibiting marked seasonal and cyclical changes. He arrived quite early in his work at the idea of communities, of natural groups of species inhabiting more or less well defined areas which could be mapped out. Of these communities he distinguished eight, and he was able to chart out in detail their distribution in the waters inside the Skaw and in the Danish fjords or sea-water broads. His communities were defined with reference to "characteristic

species"; thus a wide-spread shallow water community was known as the *Macoma* community, from the universal occurrence of the small bivalve *Macoma baltica*. Again, in deeper water, a certain community was characterised by the abundance of the ophiuroid *Amphiura filiformis*, with which was usually associated the heart-urchin *Echinocardium cordatum*, and it was called the *Amphiura filiformis* community, or the *Echinocardium-filiformis* community. The communities had fairly definite relations with depth of water, character of the bottom, and probably also with other factors such as temperature and salinity, but Petersen preferred to regard them as natural units rather than attempt to analyse all the complex conditions which determined their composition and distribution. Even more important than the physical were the biological factors that affected the composition of the communities; thus with the "producers," such as small bivalves and worms, which fed directly on the detritus produced by the decay of *Zostera*, were naturally associated the "consumers" or predatory forms which fed upon them. Petersen nowhere gives a hard and fast definition of his communities, nor attempts to analyse completely their basis of association. He was impressed by the complexity of the factors involved.

We may note in passing that one of the factors recognised by Petersen, namely the texture of the bottom soil, has been very carefully studied by Davis (26, No. 2) in the North Sea. He finds a close relation in many cases between the size of particles of the soil and the species of animals found therein, and he is inclined to substitute for the Petersen community idea the principle of Soil Associations.

For further details of the community conception the reader may be referred to **60, 61** and **62**. A useful summary account will be found in **63**.

The mapping out of communities was, however, only one part of Petersen's work. He was before all a fishery biologist. He instituted the transplantation of small plaice from the outer part of the Limfjord, where they were densely crowded and slow growing, to the inner areas, where the conditions of growth were more favourable, and this was carried out on a considerable scale with Government aid for many years. He was greatly interested in determining the amount of food available for these transplanted plaice, and came to the conclusion that the amount was by no means unlimited. He early seized upon one cardinal point which, as already indicated in Section II, is of general significance in all studies of the "overfishing" problem, namely that the yield of a fishery is dependent not only on the numbers of the stock but upon their rate of growth also, and this in its turn is of course largely governed by the amount of food available. He developed his views on the regulation of fisheries, from this essentially ecological point of view, particularly in a masterly paper published in 1922 (**64**).

Reverting to the subject of food-chains, we may briefly refer to Petersen's views as to the source of fish food in Danish waters. One striking feature of

these waters, particularly in the shallow sea-water broads or Brednings, is the extraordinary abundance of *Zostera marina* (see **65**). Petersen estimated that it covered 2000 square miles of the sea bottom inside the Skaw, and that the annual production reckoned as dry weight was no less than 8000 million kilograms. He saw in these vast *Zostera* banks the main source of the organic matter utilised by the bottom-living organisms and at second or third hand by the fish. Some of it is used direct, e.g., by browsing molluscs, but the bulk of it is utilised in its decayed and broken down form as fine detritus, which is, according to Petersen, the main food of lamellibranchs and many polychaets. For these small bivalves and worms which feed directly upon the detritus there compete many of the fish, the echinoderms, and the larger predatory molluscs and crustacea, which accordingly all rank as consumers, while the detritus feeders are the main animal producers.

Petersen made an attempt to work out roughly the total production of animal forms in the Danish waters. Starting with 24 million tons (wet weight) of plants, mainly *Zostera*, he reckoned that this produced 5 million tons of species useless for food, chiefly large forms like *Cyprina*, *Echinocardium* and *Brissopsis*, and 1 million tons of "useful" food, such as small bivalves and worms. On the "useful" food lived the predatory crustacea and gastropods, also echinoderms like the starfish, to the amount of 75,000 tons, edible fish like the plaice, whose annual production was estimated at 5000 tons, and small fish, say 10,000 tons. The cod, which lives on small fish and on the predatory crustacea and gastropods, gave a yield of 6000 tons.

Petersen gives these estimates, which are admittedly rough, in the form of a pyramid of numbers (Elton), or rather a pyramid of weights, in his paper of 1918 (**61**, p. 22). He went on the general assumption that it took 10 kg. of producers to make 1 kg. of consumers. He did not consider the plankton to be of much importance as food for bottom-living animals, though he recognised of course its value as food for pelagic fish like the herring.

It will be seen that Petersen had a sound grasp of ecological principles, and envisaged the complex problem of the production of fish as being essentially a problem of ecology.

In conclusion, let me emphasise once more that I have not attempted the well-nigh impossible task of giving a full account of the results of fishery research; I have touched very lightly upon the main problems, but I have tried to indicate the principal papers of recent date by means of which ecologists may become more familiar with the subject. There is, of course, a great deal of general work on marine biology, for instance that produced by the Plymouth Laboratory, to which I have not referred, owing to the limitation of my subject, but this work is already known to the ecologist. I hope, however, that I have said enough to prove my point that fishery research is essentially a study in marine ecology, and to give some idea of its scope, its methods and its results.

REFERENCES.

GENERAL.

A very useful general guide to the main literature on marine and fishery research is Dr E. J. Allen's "Selected Bibliography of Marine Bionomics and Fishery Investigation," published in the *Journal du Conseil International*, **1**, 1926, and also separately by A. F. Høst, Copenhagen. A current bibliography on similar lines appears in each number of the *Journal du Conseil*, which also publishes special bibliographies from time to time.

SECTION I.

(1) **Murray, Sir John** and **Hjort, Johan**. *The Depths of the Ocean*, London, 1912.

(2) **Russell, E. S.** "The work of the Fisheries Laboratory, Lowestoft." *Science Progress*, Jan. 1929, pp. 457–67.

(3) The series of *Rapports et Procès Verbaux* published by the Council at Copenhagen (A. F. Høst), particularly Vol. XLVII, 1928, the *Rapport jubilaire*, giving a review of 25 years' work.

SECTION II.

(4) **Russell, E. S.** and **Edser, T.** "The fishery statistics of England and Wales." *Journ. Roy. Statist. Soc.* **88**, 221–50, 1925.

(5) **Edser, T.** "A short account of the statistics of the sea fisheries of England and Wales." *Rapp. Proc. Verb.* **36**, Copenhagen, 1925.
English fishery statistics are published annually by the Ministry of Agriculture and Fisheries under the title "Sea Fisheries—Statistical tables," Scottish statistics in the same way by the Fishery Board. A summary of the statistics for north-west Europe is published annually by the International Council as the "Bulletin statistique."

(6) **Russell, E. S.** "Report on market measurements in relation to the English cod fishery during the years 1912–14." *Fishery Investigations* (Min. of Agric. and Fisheries), Ser. 2, **5**, No. 1, 1922.

(7) **Borley, J. O.** and Collaborators. "The plaice fishery and the war." *Fishery Investigations*, Ser. 2, **5**, No. 3, 1923.

(8) **Borley, J. O.** and **Thursby-Pelham, D.** "Report on the English plaice investigations in the North Sea during the years 1921–23." *Fishery Investigations*, Ser. 2, **7**, No. 6, 1924.

(9) **Savage, R. E.** "The relation between the feeding of the herring off the east coast of England and the Plankton of the surrounding waters." *Fishery Investigations*, Ser. 2, **12**, No. 3, 1931.

(10) **Carruthers, J. N.** "A new current-measuring instrument for the purposes of fishery research." *Journ. du Conseil*, **1**, 127–39, 1926. See also *Journ. du Conseil*, **5**, 167–91, 1930.

SECTION III.

(11) **Lea, Einar.** "Mortality in the tribe of Norwegian herring." *Rapp. Proc. Verb.* **65**, 100–117, 1930.

(12) **Hodgson, W. C.** "Investigations into the age, length and maturity of the herring of the southern North Sea." Part III. *Fishery Investigations*, Ser. 2, **11**, No. 7, 1929. *Fishing News* (Aberdeen), 22. viii. 31.

(13) "Report of the Transition Area Committee concerning plaice investigations in the Kattegat and Skagerak." *Rapp. Proc. Verb.* **71**, 1931.

(14) **Russell, E. S.** "Some theoretical considerations on the 'overfishing' problem." *Journ. du Conseil*, **6**, 3–20, 1931.

(15) **Dawes, Ben.** "Growth and maintenance in the plaice." Part I. *Journ. Mar. Biol. Assoc.* **17**, No. 1, 103–74, 1930. Part II, **17**, 877–947, 1931.

SECTION IV.

(16) **Hjort, Johan.** "Fluctuations in the great fisheries of Northern Europe." *Rapp. Proc. Verb.* 20, 1914.

(17) **Hjort, Johan.** "Fluctuations in the Year-Classes of important food fishes." *Journ. du Conseil*, **1**, 5–38, 1926.

(18) "Fluctuations in the abundance of the various year-classes of food fishes" (papers by 20 authors). *Rapp. Proc. Verb.* **65**, 1930, and **68**, 1930 (papers by six reporters).

(19) **Hansen, B. Helland.** "Statistical research into the biology of the haddock and cod in the North Sea." *Rapp. Proc. Verb.* **10**, 1909.

(20) **Russell, E. S.** "Report on market measurements in relation to the English haddock fishery during the years 1909–11." *Fishery Investigations*, Ser. 2, **1**, 1914.

(21) **Thompson, H.** "Haddock biology (North Sea). A brief survey of recent data, methods and results." *Rapp. Proc. Verb.* **54**, pp. 135–63, 1929. "Fluctuations in the North Sea haddock stock." *Rapp. Proc. Verb.* **65**, 1930. "On the possibility of effecting and utilising accurate estimates of haddock fluctuations." *Rapp. Proc. Verb.* **68**, 1930.

(22) **Hodgson, W. C.** "Prospects for the East Anglian herring fishery." *Fishing News* (Aberdeen), 28. ix. 29, 20. ix. 30 and 22. viii. 31.

(23) **Johansen, A. C.** "On the influence of the currents upon the frequency of the mackerel in the Kattegat and adjacent parts of the Sound." *Medd. Komm. Havunders.* Ser. Fiskeri, **7**, No. 8, 1925.

(24) **Jensen, A. J. C.** "On the influence of hydrographical factors upon the yield of the mackerel fishery in the Sound." *Rep. Danish Biol. Sta.* **36**, 1930.

(25) **Pettersson, Otto.** "Hydrography, climate and fisheries in the Transition Area." *Journ. du Conseil*, **1**, 305–21, 1926.

(26) **Davis, F. M.** "Quantitative studies on the fauna of the sea bottom. No. 1. Preliminary investigation of the Dogger Bank." *Fishery Investigations*, Ser. 2, **6**, No. 2, 1923. "No. 2. Results of the investigations in the southern North Sea." *Fishery Investigations*, Ser. 2, **8**, No. 4, 1925.

(27) **Hagmeier, A.** "Eine Fluktuation von *Mactra (Spisula) subtruncata*, Da Costa, an den ostfriesischen Küste." *Ber. deutsch. wiss. Komm. Meeresforsch.*, N.F. **5**, No. 3, 126–55. 1930.

Section V.

(28) **Wollaston, H. J. B.** "The spawning of the plaice in the southern part of the North Sea in 1913–14." *Fishery Investigations*, Ser. 2, **5**, No. 3, 1923. "Plaice-egg production in 1920–21." *Fishery Investigations*, Ser. 2, **9**, No. 2, 1926.

(29) **Damas, D.** "Contribution à la Biologie des Gadides," and **Schmidt, Johs.** "The distribution of the pelagic fry and the spawning regions of the gadoids in the North Atlantic from Iceland to Spain." *Rapp. Proc. Verb.* **10**, 1909.

(30) **Graham, Michael** and **Carruthers, J. N.** "The distribution of the pelagic stages of the cod in the North Sea in 1924 in relation to the system of currents." *Fishery Investigations*, Ser. 2, **8**, No. 6, 1925.

(31) **Graham, Michael.** "The annual cycle in the life of the mature cod in the North Sea." *Fishery Investigations*, Ser. 2, **6**, No. 6, 1924.

(32) **Carruthers, J. N.** "The flow of water through the Straits of Dover as gauged by continuous observations at the Varne Lightvessel." *Fishery Investigations*, Ser. 2, **11**, No. 1, 1928.

(33) **Carruthers, J. N.** "The water movements in the southern North Sea. Part I. The surface drift." *Fishery Investigations*, Ser. 2, **8**, No. 2, 1925. "Part II. The bottom currents." *Fishery Investigations*, Ser. 2, **9**, No. 3, 1926.

(34) **Carruthers, J. N.** "Further investigations upon the water movements in the English Channel. Drift-bottle experiments in the summers of 1927, 1928 and 1929, with critical notes on drift-bottle experiments in general." *Journ. Mar. Biol. Assoc.* **17**, 241–75, 1930.

(35) **Tait, J. B.** "The surface water drift in the northern and middle areas of the North Sea and in the Faroe-Shetland Channel," Parts I and II. *Scientific Investigations* (Fishery Board for Scotland), 1930, Nos. 2 and 4.

(36) **Carruthers, J. N.** "New drift bottles for the investigation of currents in connection with fishery research." *Journ. du Conseil*, **3**, 194–205, 1928. Also in *Fisheries Notice* (M.A.F.), No. 16, 1931.

(37) **Lumby, J. R.** "The surface sampler." *Journ. du Conseil*, **2**, 332–42, 1927; **3**, 340–50, 1928; and **4**, 281–3, 1929.

(38) **Lumby, J. R.** "The salinity and water movements in the English Channel and Southern Bight during the period 1920–23." *Fishery Investigations*, Ser. 2, **7**, No. 7, 1925.

(39) **Böhnecke, G.** "Salzgehalt und Strömungen der Nordsee." *Veröff. Inst. Meereskunde*, N.F., No. A 10, Berlin, 1922.

(40) Lumby, J. R. and **Carruthers, J. N.** "An experiment dealing with the interpretation of salinity distribution charts." *Journ. du Conseil,* **3,** 176–90, 1928.

(40a) Sund, O. "Nyt Fiskertermometer." *Fiskets Gang* (Bergen), 10. ii. 26.

(41) Lumby, J. R. and **Atkinson, G. T.** "On the unusual mortality amongst fish during March and April, 1929, in the North Sea." *Journ. du Conseil,* **4,** 309–32, 1929. See also papers by A. C. Johansen and H. Blegvad in *Rep. Danish Biol. Sta.* **35,** 1929.

(42) Ostenfeld, C. H. "Résumé des Observations sur le Plankton des Mers explorées par le Conseil pendant les Années 1902–8." *Bulletin Trimestriel,* Pte **4,** 1931.

(43) Hardy, A. C. "Notes on the Atlantic Plankton taken off the east coast of England in 1921 and 1922." *Public. de Circonstance* (I.C.), No. 78, 1923. "The Herring in relation to its animate environment. Part II. Report on trials with the Plankton indicator." *Fishery Investigations,* Ser. 2, **8,** No. 7, 1925.

(44) Savage, R. E. "The influence of *Phaeocystis* on the migration of the herring." *Fishery Investigations,* Ser. 2, **12,** No. 2, 1930.

(45) Hardy, A. C. "A new method of Plankton research." *Nature,* **118,** 630, 1926.

(46) Savage, R. E. "The Plankton of a herring ground." *Fishery Investigations,* Ser. 2, **9,** No. 1, 1926.

(47) Hickling, C. F. "The natural history of the hake." Parts I and II. *Fishery Investigations,* Ser. 2, **10,** No. 2, 1927.

(48) Bull, H. O. "Studies on conditioned responses in fishes." Part I, *Journ. Mar. Biol. Assoc.* **15,** No. 2, 1928; Part II, *Journ. Mar. Biol. Assoc.* **16,** No. 2, 1930.

(48a) Graham, Michael. "Some Problems in Herring Behaviour." *Journ. du Conseil,* **6,** 252–65, 1931.

SECTION VI.

(49) Lebour, Marie V. "The Food of young clupeoids." *Journ. Mar. Biol. Assoc.* **12,** No 3, 1921. "The food of young herring." *Journ. Mar. Biol. Assoc.* **13,** No. 2, 1924.

(50) Hardy, A. C. "The herring in relation to its animate environment. Part I. The food and feeding habits of the herring." *Fishery Investigations,* Ser. 2, **7,** No. 3, 1924.

(51) Jespersen, P. "Investigations on the food of the herring in Danish waters." *Medd. f. Komm. Havundersøg.* Serie Plankton, **2,** No. 2, 1928.

(52) Lebour, M. V. "The food of Plankton organisms. I." *Journ. Mar. Biol. Assoc.* **12,** No. 4, 1922. "The food of Plankton organisms. II." *Journ. Mar. Biol. Assoc.* **13,** No. 1, 1923.

(53) Atkins, W. R. G. "A quantitative consideration of some factors concerned in plant growth in water." *Journ. du Conseil,* **1,** 99–126 and 197–226, 1926. Also many papers in *Journ. Mar. Biol. Assoc.*

(54) Gaarder, T. and **Gran, H. H.** "Investigations of the production of Plankton in the Oslo Fjord." *Rapp. Proc. Verb.* **42,** 1927.

(55) Schreiber, E. "Die Reinkultur von marinen Phytoplankton und deren Bedeutung für die Erforschung der Produktionsfähigkeit des Meerwassers." *Wiss. Meeresunters.* Abt. Helgoland, **16,** No. 10, 1927.

(56) Marshall, S. M. and **Orr, A. P.** "The relation of the Plankton to some chemical and physical factors in the Clyde Sea area." *Journ. Mar. Biol. Assoc.* **14,** No. 4, 1927. "A study of spring diatom increase in Loch Striven." *Journ. Mar. Biol. Assoc.* **16,** No. 3, 1930.

(57) Poole, H. H. and **Atkins, W. R. G.** "On the penetration of light into sea-water." *Journ. Mar. Biol. Assoc.* **14,** No. 1, 1926. Also in **15,** 2, 1928, **16,** 1, 1929, and **16,** 2, 1930.

(58) Brandt, K. "Stickstoffverbindungen im Meere. I." *Wiss. Meeresunters.* Abt. Kiel, **20,** 1927.

Gran, H. H. "The production of Plankton in the coastal waters off Bergen." *Rep. Norweg. Fishery and Marine Investigation,* **3,** No. 8, 1927.

Gran, H. H. and **Ruud, B.** "Untersuchungen über die im Meerwasser gelösten organischen Stoffe und ihr Verhältnis zur Planktonproduktion." *Norske Videnskaps-Akad. Oslo,* Matem.-Naturvid. Kl., 1926, No. 6.

Harvey, H. W. "*Biological Chemistry and Physics of Sea Water.*" Cambridge, 1928.

"The estimation of phosphates and nitrogenous compounds in sea water." *Rapp. Proc. Verb.* **53,** 1929. (Papers by Brandt, Buch, Giral, Harvey, Schreiber, Sund, Wattenberg, with Appendix on methods.) Also **75,** 1931.

(59) Blegvad, H. "Food and conditions of nourishment among the communities of invertebrate animals found on or in the sea-bottom in Danish waters." *Rep. Danish Biol. Sta.* **22,** 1914.

(60) Petersen, C. G. J. and **Boysen-Jensen, P.** "Valuation of the sea. I. Animal life of the sea bottom, its food and quantity." *Rep. Danish Biol. Sta.* **20,** 1911.

Petersen, C. G. J. "Valuation of the sea. II. The animal communities of the sea bottom and their importance for marine zoogeography." *Rep. Danish Biol. Sta.* **21,** 1914.

(61) Petersen, C. G. J. "The sea bottom and its production of fish food. A survey of the work done in connection with valuation of the Danish waters from 1883–1917." *Rep. Danish Biol. Sta.* **25,** 1918.

(62) Boysen-Jensen, P. "Valuation of the Limfjord. I." *Rep. Danish Biol. Sta.* **26,** 1919.

(63) Petersen, C. G. J. "A brief survey of animal communities in Danish waters." *Amer. Journ. Sci.* **7,** 343–54, 1924.

(64) Petersen, C. G. J. "On the stock of plaice and the plaice fisheries in different waters: a survey." *Rep. Danish Biol. Sta.* **29,** 1922.

(65) Ostenfeld, C. H. "On the ecology and distribution of the grass wrack (*Zostera marina*) in Danish waters." *Rep. Danish Biol. Sta.* **16,** 1908.

NOTES ON THE NATURAL REGENERATION
OF WOODLAND IN ESSEX

By R. S. ADAMSON.

THE purpose of the following notes is principally to draw the attention of plant ecologists to the region of high ground around Danbury in Essex, between Chelmsford and Maldon, which is of considerable interest in providing an unusually complete series of stages in the natural regeneration of forest communities, and of which no ecological description appears to exist. The village of Danbury may be taken as the centre of an area remarkable for the general and rapid regeneration of natural woodland (Ordnance Survey 1 in. map, No. 108). This natural regeneration of woodland occurs on the summit and slopes of a ridge which rises from 300 to 350 ft. above sea-level. The summit of the ridge, which exceeds 300 ft. in altitude, forms a narrow strip running north and south for a distance of about 2 miles. The ground falls away from this on all sides. The areas where forest regeneration occurs are covered by glacial sand, loam and clay associated with the boulder clay, and lie on the ridge itself or on the slopes, but are all above the 200 ft. contour line.

On this elevated ground are several areas of common land, of unoccupied land, and of neglected pasture. To the south is Danbury Common: Lingwood Common is near the centre of the area: to the north-east is Woodham Walton Common. The estates of Riffam's and of Danbury Park contain several tracts of unutilised pasture. Of these areas Danbury Common and Lingwood Common are real common lands over which grazing rights exist and are exercised. Woodham Walton Common is a common only in name. Though crossed by rights of way it is privately owned and not used for grazing. The remaining areas are also private property.

The soil varies from very heavy clay to a flint gravel with every stage of transition. The different types of soil occur on closely adjacent areas. On the ridge much of the clay soil becomes very wet and water-logged in the winter. In a general way the valleys and the flat-topped ridges have the heavier soils, the slopes the lighter.

In this area true woodland vegetation is not very abundant, though several examples occur. Much of the portion marked green on the Ordnance Survey map is developing rather than established woodland. The woodlands are of oak standards, associated with birch on light soils, and with hornbeam and locally hazel coppice on the heavier. These woods belong to the *Quercus sessiliflora-Carpinus* type described by Salisbury for Hertfordshire (cf. This JOURN. **6**, 14, 1918). While *Q. sessiliflora* is much the more abundant tree, *Q. robur* is also present.

It is no part of the present purpose to describe these woodlands: all that will be attempted is to give an outline of some of the salient features of the developmental stages which are here so abundant. No details can be given, and very little can be considered beyond the relationships of the woody plants.

The regenerative successions or subseres fall into two groups owing to the presence or absence of an interfering factor in the form of grazing or otherwise. Development without interference can be traced on Woodham Walton Common and on the private lands. On the common land, however, the direct line of development is interfered with to a greater or less extent by grazing, cutting or burning. In such cases the series of phases in the regeneration is complicated or even modified to a large extent, both in the characters of the developmental communities and in their finer relations.

On these commons there are to be seen, in fact, what Godwin has termed "deflected successions" (*Nat. Hist. Wicken Fen*, 1930). Development which is not complicated by interference will be treated first, as this provides the basis upon which the elucidation of the more complicated cases is founded.

The actual stages in the succession, of course, may vary with the local conditions of soil, etc., but certain features are common to all of them. The pioneer stage of woody plants depends on the community that is being invaded. On ground that has been cleared of woodland and on which a mixed herb community exists, the invasion of trees and shrubs is direct by seeding. The pioneers are *Betula* (*B. alba* on gravel, *B. pubescens* generally more abundant), *Salix cinerea* and *Quercus*, especially *Q. sessiliflora*. Together with these trees are *Rubus caesius* and other species, *Rosa* spp., *Crataegus*, etc. *Ulex europaeus* and *Cytisus scoparius* are common on the less clayey soils.

In such cases birch and oak soon attain a dominance over the others and gradually form closed thickets. Many examples of thickets of young trees of oak and birch 10–15 ft. in height may be met with. The two trees either occur together or in alternating pure patches. Within these thickets are *Rubus, Rosa* (which with *Pteridium* may form an undergrowth of great density), *Crataegus* (fairly common), *Ulex* and *Cytisus* becoming drawn up and gradually suppressed. Other trees or shrubs are *Salix cinerea* and, less frequently, *Corylus* and *Carpinus*.

A somewhat different series of phases and a series occupying a longer period of time occurs where the area is originally occupied by grassland. The grassland is dominated by *Agrostis tenuis* with varying proportions of *Festuca* (probably *F. rubra* agg.) and other species. When such grassland is left without grazing, cutting, or other form of interference, a gradual invasion occurs by *Rubus* (*R. caesius* and other spp.) and *Rosa*, but especially the former. The Rubi with their trailing shoots spread through and over the grasses and assume a local dominance. These islands form a nidus for the establishment of various woody plants, of which *Salix cinerea, Quercus sessiliflora* and *Betula* are the commonest. Others are *Crataegus* and rarely *Corylus* and *Carpinus*.

Fraxinus and *Salix caprea* are confined to permanently wet places. *Ulex europaeus* and *Cytisus scoparius* form the first invaders of the grassland on gravelly or light soils, and these largely replace *Rubus*. The *Rubus* islands with their associated bushes and young trees gradually increase in density and size, the trees assume dominance over the low bushes, and the patches unite together.

As an example of the time factor in the earlier stages one case may be quoted. On the summit of the ridge, about a mile to the north of Danbury village, is an almost level stretch of heavy clay soil. This area was occupied during the war by an encampment of huts. As a result of the trampling involved the vegetation was almost completely eliminated, and woody plants entirely. After the removal of the camp in 1919, the ground was divided into plots for sale as building land. Some of these have remained untouched ever since. The present condition is a dense covering of grass, chiefly *Agrostis tenuis*, which forms a dense growth 6–12 in. in height. Interspersed through this are colonies of *Rubus*, chiefly *R. caesius*, but other species also. These *Rubus* patches now occupy more than a third of the area. Associated with *Rubus* are scattered plants of the following:

Betula alba	Quercus sessiliflora
B. pubescens	Rosa arvensis
Cytisus scoparius (l)	Rosa spp.
Crataegus oxyacantha	Salix cinerea
Carpinus betulus (r)	Ulex europaeus

The grassland which is thus invaded is not a close turf. The grasses form long shoots that are decumbent but do not root at the nodes. Where such *Agrostis* grassland is cut or grazed, a turf is formed owing to the close growth and rooting of the side shoots. In other cases the grassland, previous to the invasion of woody plants, is of the tussock variety. In most of the grassland areas, where this type of invasion is occurring, the conditions are rather different along the hedges or the boundaries of existing woodlands. Here a marginal zone of direct invasion is common.

These successions on grassland may be summarised as forming the following stages:

(1) Ungrazed (*Agrostis*) grassland without definite turf.
(2) *Rubus* thicket.
(3) Shrubs and trees established under the shelter of *Rubus*.
(4) Oak (*Q. sessiliflora*) and birch (*Betula pubescens* and *B. alba*) thickets.
(5) Woodland of oak and birch.

The general succession *Agrostis* → *Rubus* → oak-birch woodland occurs on all soils, from heavy clays to sandy loams.

The transition from stage 3 to stage 4 is much slower in time than from stage 1 to stage 3. In stage 2 *Rubus* may be replaced by *Ulex* and to a less extent by *Cytisus*. These may become definitely dominant, and the advance to the subsequent stages is then slower. Again, as the later stages are reached

and a canopy is formed, *Ulex* and *Cytisus* are gradually eliminated while *Rubus* persists as an understorey.

Certain features of these regenerations may be noticed. The pioneer trees in all cases seem to be oak and birch. The hornbeam is generally absent in the early phases, and where present is rare. This tree would seem to require definite woodland cover for establishment. The absence of hornbeam in the earlier stages is not in any way accounted for by absence or scarcity of seed parents. Hornbeam is exceedingly common in all the hedges, and these are allowed to grow 12 or 15 ft. high, and flower and fruit regularly and freely. In one field where such regeneration was occurring, young oaks and birches were frequent, but only a single small hornbeam was noticed. The surrounding hedges were largely hornbeam, while the nearest parent birch was about 200 yards distant. (In this connection cf. Salisbury "Ecology of Scrub," *Trans. Herts. Nat. Hist. Soc.*, 1918.) *Corylus* is even less frequent than *Carpinus*, and seems quite confined to those places where a canopy is formed. It is nowhere abundant. This is in marked contrast to the re-colonisation of woodland on chalk soils (cf. Adamson, "The Woodlands of Ditcham Park," This JOURN. 1922).

Certain other trees and shrubs which are not uncommon in established woodland or in hedges appear to take little or no part in the re-colonisation of open ground. Among these may be noticed *Pyrus malus, Sorbus torminalis, Sambucus nigra* and generally also *Prunus spinosa. Populus tremula* is locally vigorous in wet places. *Acer pseudoplatanus*, though exceedingly abundant in some of the woodlands, does not spread into the open at all, and the same applies to *Castanea sativa*. On the other hand, *Quercus cerris* is spreading rapidly on some of the lighter soils and locally replaces *Q. sessiliflora. Sorbus aucuparia* is present but never at all common.

On the common lands where grazing has been carried on, different conditions are found. This is especially the case with Danbury Common, which is used for the pasturage of cattle and of goats. Burning of this common is also not infrequent. The greater part is covered by alternating communities dominated by *Ulex europaeus* and *Pteridium aquilinum* respectively. Along with the *Ulex* occur *Rubus, Rosa, Prunus spinosa, Crataegus, Cytisus*, and, very occasionally, small trees of *Quercus sessiliflora* and *Betula*. These, however, occur as more or less isolated plants, and even though *Rubus* may form tangles there are no obvious signs of any advance of the succession. The low bush community which is definitely dominated by *Ulex* appears practically stable under the conditions existing.

In some places, however, and especially on the portions of the common more remote from the village, scrub woodland is developed. It exists in the form of thickets, often exceedingly dense, of *Crataegus* and *Prunus spinosa*. These are mixed with, and to some extent bound together by, *Rubus* and *Rosa*. Among these spiny thickets are young oak trees. *Ulex* occurs only round the

margins. In the larger patches of this nature there occur also *Carpinus*, *Betula*, *Salix cinerea* and *Corylus*. These undoubtedly represent the beginnings of the woodland climax.

The communities mentioned represent in essentials the same successional phases as those described above, but modified and "deflected" owing to interference. Where this is severe the stabilisation of the *Ulex* community results. This is assisted by the periodic burning as well as by grazing. Where the grazing intensity is less a further advance occurs. The temporary dominance of the spinous shrubs is here correlated with their relative immunity, the other trees becoming established under their shelter.

Under these conditions there is not nearly such a decided difference in behaviour between the oak and the hornbeam. That this, however, is itself the result of the destruction of young plants may be gathered from the fact that the hornbeam is confined to the sheltered thickets while occasional young oaks occur outside.

Further confirmation of this explanation of the differences between the development on Danbury Common and that on ungrazed land is obtained from a study of Lingwood Common.

This common occupies the side of a valley and is partly on a steep slope. The vegetation shows a condition intermediate between that of the ungrazed areas and the grazed Danbury Common. The soil varies from a flint gravel at the top of the slope to a heavy clay in the valley. *Ulex* is generally absent, and nowhere dominant. On the heavier soils there occur thickets of spinous shrubs with associated trees, exactly like those on Danbury Common, but they are more frequent and cover larger areas. The gravelly portions are covered by a scrub growth of *Quercus sessiliflora* with local *Betula* and associated *Rubus, Rosa, Crataegus*, etc. *Carpinus* and *Corylus* occur, but are rare. *Calluna* is dominant on the most stony patches. Here there appears to be direct invasion of oak and birch, but the stages have been upset to a considerable extent by bracken cutting and, still more, by wood-cutting.

The above notes make no claim to give a complete or final account of the successions leading to the re-establishment of woodland in this area. Their purpose is rather to call attention to the existence of a remarkably good series of examples which would certainly repay study. The area is in no way remote, and is already in part threatened by the activities of the builder.

STUDIES IN THE ECOLOGY OF WICKEN FEN

II[1]. THE FEN WATER TABLE AND ITS CONTROL OF PLANT COMMUNITIES

BY H. GODWIN AND F. R. BHARUCHA.

(With eighteen Figures in the Text.)

CONTENTS.

I. THE FEN WATER TABLE.

THE movements of the water table in the fen are subject to daily and seasonal variation and to alteration by rainfall, plant transpiration and the factors affecting the drainage system. The general character of these relationships as applied to one or two special points in the fen only has already been indicated in detail in the preceding paper (1), and we now propose to consider the way in which these principles apply to the fen as a whole.

A. METHOD.

It was clear that the best means of achieving such knowledge of the movement of the fen water table lay in the use of a large number of automatic water-level recorders set up in different chosen situations about the fen, with their true relative heights determined by accurate levelling. The cost of such instruments has precluded their use in numbers, but one has been set up in the fen for two and a half years and a second for some months. The absence of further automatic level recorders has raised the significant question as to how far the record taken in one part of the fen holds true for any other part, or if it may be satisfactorily interpreted so as to yield useful information about such another part. This question has been met by the use all over the fen of water-level pits which could be visited and read at suitable times. Each pit was about 70 cm. long, 20 cm. wide and up to about 80 cm. deep. The level of the peat surface on the sharply cut edge of each long side was carefully measured (by vertical height from the water surface in the pit), and so a close estimate was obtained of the position of average soil level (A.S.L.). A vertical oak stake about 220 cm. long was driven deeply into the floor of the pit, so that only the top of the stake appeared above A.S.L. and so that two large nails projecting from the stake were just at A.S.L. Above A.S.L. for about 20 cm., and below it for about 60 cm., the stake was studded with small brass nails at intervals of 1 cm. apart. The stake served as a ready means of measuring the distance between average soil level and the water table. It has already been shown (1) that the water level in such pits does really represent the water level in the immediately surrounding fen.

The distribution of the pits was controlled by two objectives: partly they were distributed so as to be situated in different typical examples of various well-marked fen communities, and partly they were placed so as to give an index to the effect of drains and lodes, etc., on the variation in water level about the fen. Their distribution is seen on the map (Fig. 1).

From the point of view of the effect of the rising and falling water table upon plant life, the datum it is desirable to know is the distance between average soil level and the water table throughout the year: this can always be measured in each pit, whatever may be the relationship of absolute height of soil and water level between one pit and the next. Thus for long it was not

considered necessary to know the true relative heights of the average soil level in the various pits over the fen. Later on it became clear that, from the
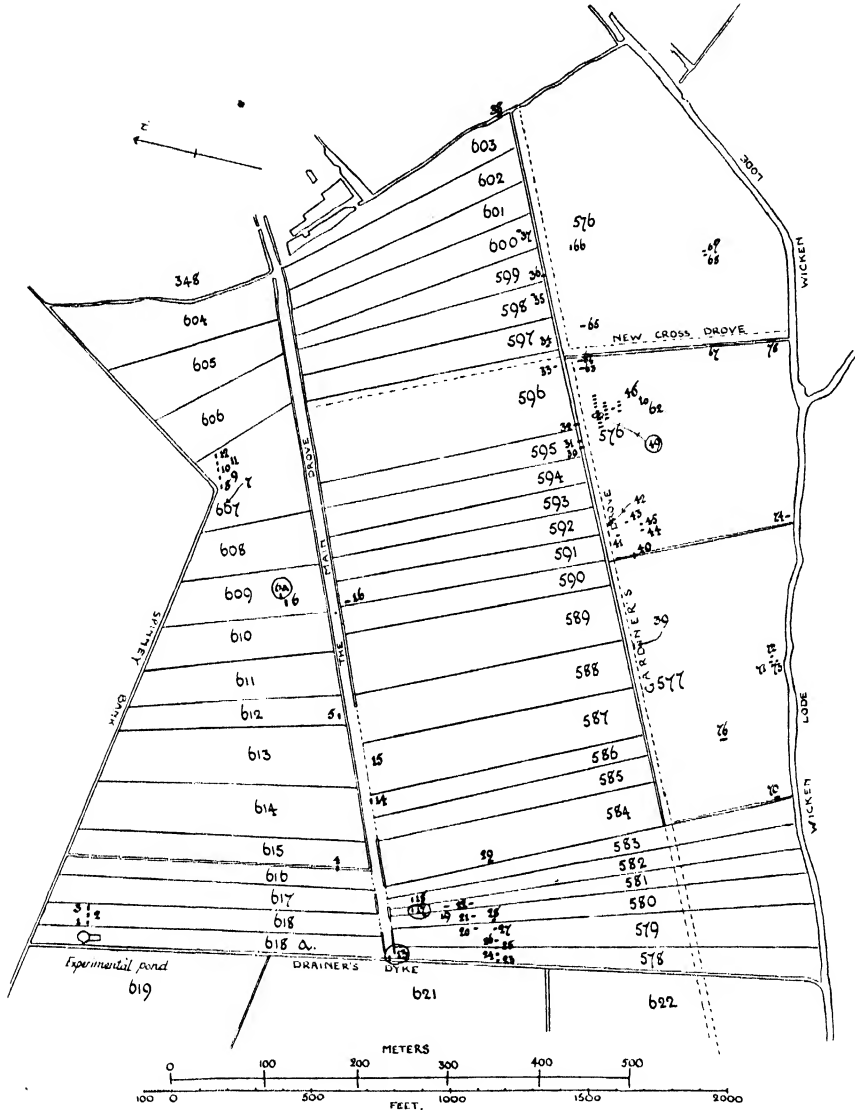
FIG. 1. Map of Wicken Sedge Fen showing the position of the water-level pits (numbered 1 to 76) in relation to droves, dykes and strips of land once under separate ownership. The pits indicated by ringed numbers (6a, 13, 17 and 49) are those used with special water-level recording apparatus (see text).

point of view of elucidating the drainage relations of the fen, it was essential to know the true relative height of the water table in all the pits at the same time. This was accomplished by carrying out a levelling survey of the pits

by means of a Y-level and a levelling staff, so that the true relative height of the A.S.L. index on the measuring stake of each pit was established to within 1 or 2 cm. A selection of a few typical results is given in Table I.

Table I.

Pit No.	Plot No.	Type of vegetation	True relative height cm.*	Comments
17	581	Litter	+ 0·5	Permanent recorder pit
18	582	,,	+ 4·0	
19	581	,,	+ 4·0	
20	579	Mixed sedge	+ 1·0	
21	580	,,	− 2·0	
22	581	Litter	− 3·0	
23	578	(Drainers' dyke)	+15·0	Standard for dyke levels
24	578	(Bank of Drainers' Dyke)	+12·0	
25	578	Mixed sedge	+ 9·0	
26	579	,,	+10·5	
27	579	,,	+13·5	
28	580	,,	+ 6·5	
29	584	,,	+ 2·0	
30	595	Pure sedge	−30·0	Dyke
31	595	,,	−28·0	Dyke
32	596	,,	−30·0	Dyke
33	596	Carr with *Cladium*	− 1·0	Cleared in 1929–30
34	597	Mixed sedge	− 7·5	
35	598	Carr with *Cladium*	− 3·0	
36	599	*Carex elata*	−25·0	Dyke
37	600	Carr with *Cladium*	+ 1·5	

* I.e. height of soil level above or below the horizontal plane called fen zero level.

The levelness of the fen, as shown by the figures of the levelling survey, is extremely striking. With the exception of the dykes and their banks, it rarely exceeds a range of 20 cm. on either side of the arbitrary zero level. Such variation is of almost the same order as can be found among the tussocks of a single square metre of the *Molinia*-dominated "litter."

The true relative height of the A.S.L. index in each pit afforded a means of working out every water level reading in terms of its true relative height also, and such values have been much used in expressing drainage relations in the fen.

The earliest water level readings were taken during six days between November 8 and 20, 1928, and were limited to 31 pits. The next four readings, this time in 47 pits, were taken in June, November and December, 1929 and in February, 1930. By May 1, however, 74 pits had been dug and very frequent readings have been taken in all of them from that date onwards. On June 8 the number was increased to 79. The actual data occupy too much space to be given in full. All that it will be possible to do here is to use selected data to illustrate the main features of the water table behaviour in different parts of the fen under varying conditions through the season

B. EFFECT OF DRAINAGE, RAINFALL AND TRANSPIRATION.

(a) *Observations of May*, 1930.

The simplest introduction to a discussion of the combined action of these factors will be a description of a particular set of observations made during May, 1930. A series of pits had been dug at right angles to Drainers' Dyke and at different distances from it. Their distribution is shown in Fig. 2.
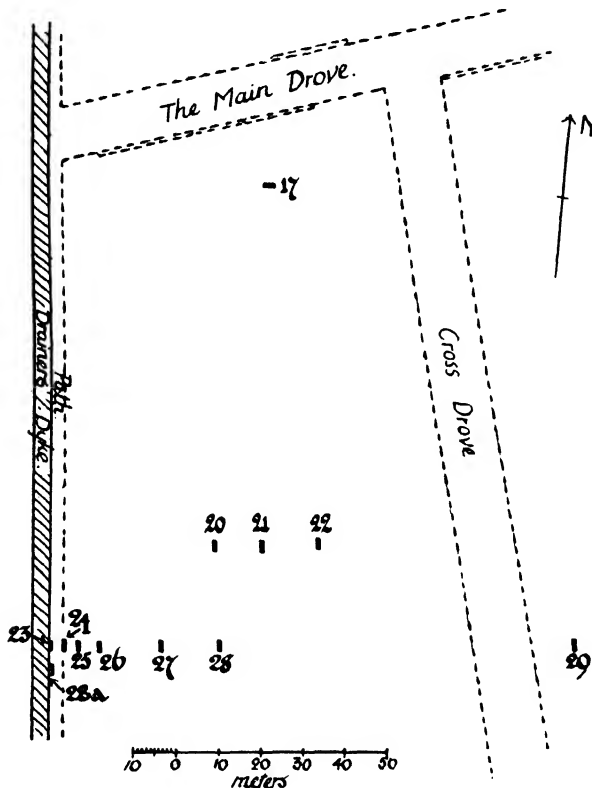
FIG. 2. Disposition of the pits dug at varying distances from Drainers' Dyke, as a means of elucidating the effect of the dyke on the fen water table.

The true relative height of the A.S.L. index in each pit was found by levelling survey. In this way a true profile of the soil surface could be obtained. Each day over a long period the water level was read in each pit (that is the distance between A.S.L. and the water level), and from this it was possible to find how for each day the soil water table differed from a true horizontal plane. This is shown in the diagrams of Fig. 3.

It was extremely fortunate that during the first few days of the experiment an altogether unusual range of water-level conditions obtained on the

fen. The experiment began on May 1 after a long period without rain, and the readings obtained on that day and on May 2, 3, 4 and 5, which were also practically dry, show the same form of water table (see Fig. 3). It is striking that the water table is not quite flat but is convex, curving down to the level of open water in Drainers' Dyke. The fall is, however, only about 5 cm. and scarcely affects more than the land within 50 m. of the dyke.
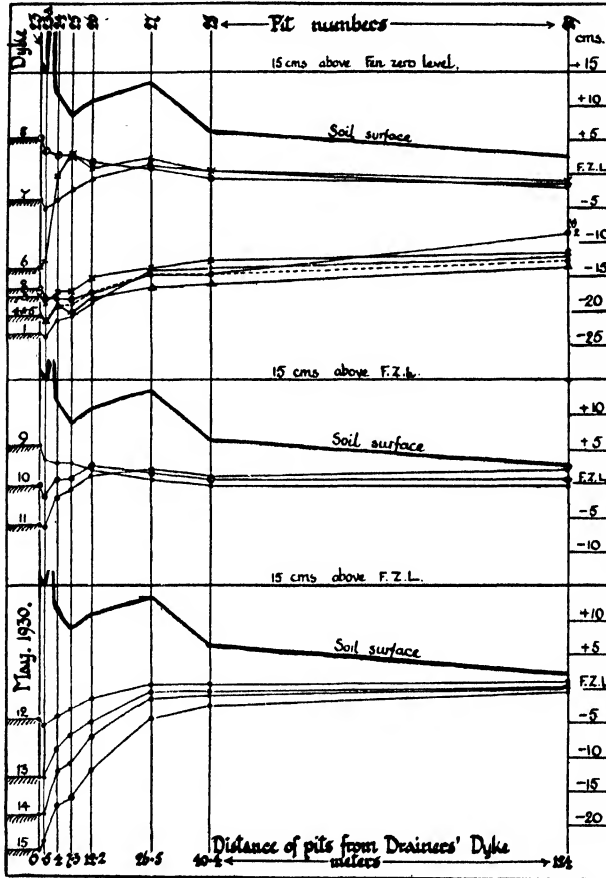
FIG. 3. Diagram showing the water-level behaviour in the fen lying within 125 m. of Drainers' Dyke during the period May 1 to May 15, 1930. (See description in text, p. 162).

(1) Rain.

Between the readings of May 5 and 6 it rained exceptionally heavily, and in the readings of May 6 interesting results are apparent:

(1) In the open lode the level had risen 7 cm., but everywhere else in the fen the rise had been far greater. This difference was certainly due to the rain filling up the air spaces of the peat in the second case, and falling into an open vessel (i.e. the dyke itself) in the first case.

(2) There is evidently the beginning of a sharp drainage gradient between fen and lode.

(2) *Rising drain levels.*

The exceptionally heavy rains of May 5 and 6 caused the valley of the river Cam to be in danger of flooding, and the sluice gates at Upware were accordingly closed to keep back all the Wicken drainage water. This therefore accumulated, and on May 7 and 8 the lodes and drains showed a water level even higher than that of the Sedge fen itself. This water, we must emphasise, came mainly from sources outside the fen itself, i.e. from Monk's Lode and neighbouring cultivated land. On May 8 the fen water table was therefore saucer shaped, with water visibly running into the fen through small breaks here and there in the lode banks.

(3) *Falling drain levels.*

This most unusual condition lasted a very short time only, for with the subsidence of the Cam, the Upware sluices were set at their normal level, and the water level in lodes and drains fell almost continuously until May 15. It will be seen that the form of the fen water table then had become convex again, that of an upturned saucer, and showed rapid drainage of the marginal belts into the drainage channels. In comparison with the marginal belt it is interesting to note how slowly the water table is falling in the pit 124 m. from the lode. Here the fall is 0·5 cm. per day, and this is probably due more to transpiration than to drainage into the lodes. It would take upwards of 20 days for this fall to restore the original condition upset by 1 day's heavy rain.

(4) *General conclusions.*

The data suggest that it would be profitable to consider the fen from the drainage point of view as composed of two regions (1) very small, forming a belt not more than 25 m. wide round all the large open drainage channels, and (2) a much larger area comprising the rest of the fen.

The former area is susceptible essentially to fluctuations in levels in lodes and drains. After heavy rains the water table very rapidly falls, so that the water-logging is never long maintained in the upper layers of the soil: exceptionally we may find the water level of such areas raised by flow of water from outside into the fen. The latter area (i.e. the interior of the fen) is scarcely affected at all by the changing water level of the drainage channels. It is determined chiefly by the balance between rainfall and evaporation (which is mainly here transpiration).

(5) *Drainage data over the fen as a whole, May,* 1930.

The daily water-level readings from May 1 to May 17 were taken not only in the series of pits mentioned above, but over the fen as a whole, and they afford an excellent opportunity of comparing the drainage relationships of

various parts of the fen where pits have been dug. In Fig. 4 are shown the rise and fall of level in a number of representative pits, throughout the period from May 1 to 17; and the course of events in the extreme cases before mentioned, i.e. Drainers' Dyke itself, and pit No. 29 situated 124 m. from Drainers' Dyke, can easily be followed. The rise continued from May 6 to 8,
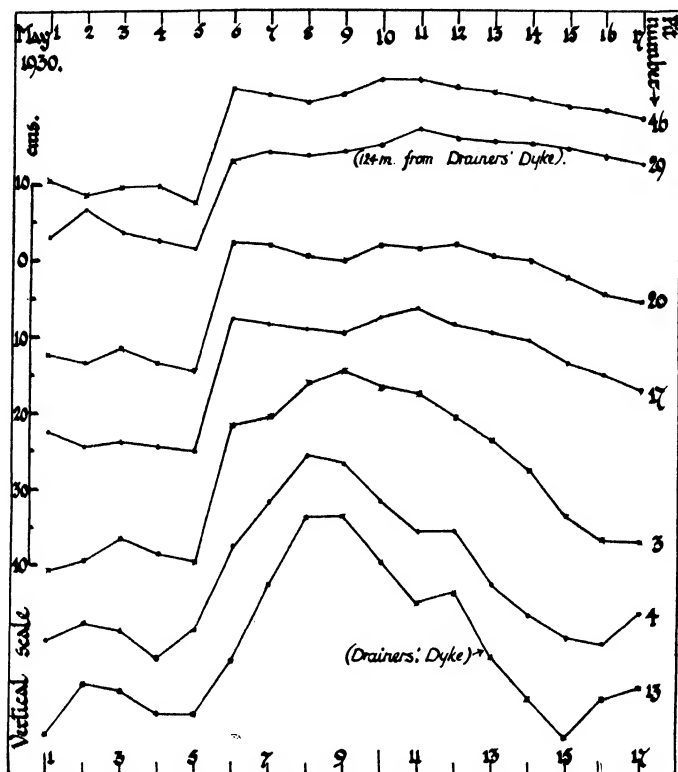
Fɪɢ. 4. Diagram to show the effect of rainfall, drainage, etc., on the height of the water table, as shown by a selected number of pits in different parts of the fen during the period May 1 to May 17, 1930. (See description in text, pp. 164, 165.) In the diagram there is no attempt made to convey the relative heights of the water table in different pits, and the vertical scale for each has a different origin.

and the very rapid fall after May 9, especially characterise the behaviour of the level in Drainers' Dyke. Pits in different places on the fen follow one or the other curve according to their situation.

(*a*) Pit 4. This is a ditch connected with the drainage system and behaving much like Drainers' Dyke.

(*b*) Pit 3. This shows the sudden rise due to rain occupying air spaces in the peat, but otherwise behaviour similar to that of Drainers' Dyke. In fact it is 30 or 40 m. from the dyke but close to a large experimental pond which is connected with it.

(c) Pit 20. This is a pit 40 m. from Drainers' Dyke, and it shows the influence of the dyke only in that after May 10 the level falls rather more rapidly than in No. 29.

(d) Pit 46. This is a pit a considerable distance from open drainage channels: in form the curve closely resembles that of No. 29 as might be expected, and it can be taken as representing the greater part of the fen area which is distant from the drainage channels.

(e) Pit 17. This is the curve for the pit containing the permanent water-level recorder and consequently is of considerable interest. Its form closely resembles that of No. 11, although it is 50 m. and not 40 from Drainers' Dyke. It is, however, probably affected somewhat by the presence, within a few metres of it, of large old filled-in dykes, no longer openly connected to Drainers' Dyke. The significance of this curve is that the water-level records taken here must always be interpreted as being somewhat affected by proximity to drainage channels. The water level will rise here at the same time and as high here as elsewhere on the fen when it rains, but it will subside here rather more rapidly afterwards than in pits in the middle of the fen. Data given in the previous paper permit us to add that drainage in from the lode will often tend to cause a rise in water level here which is not evident farther towards the centre of the fen.

Without giving data for other pits on the fen we may say that the majority showed water-level curves of the types mentioned here. A few exceptional cases were partly explicable in terms of the following considerations.

(a) Where a rise in the water table brings open water above the peat level, the rise due to rain is not so great and does not continue as long as where no free water shows above the peat. This effect can be seen in hummocky ground when the water table approaches average soil level, and in ridged and furrowed land.

(b) A similar effect can be seen where any large low area drains another, e.g. where a 10 cm. rise in the water level brings open water into one area and not to the next, the latter will drain into the former because of the higher level in the latter.

We may at this stage recall some main considerations about the behaviour of the water table.

(1) The rise due to rain is general over the whole fen (though more in some parts than others), but the fall is locally different.

(2) Save in the marginal 50 m. beside big drains the fall in water level is very slow all over the fen, even with a low level in the dykes. That is, the fen takes a very long time to drain.

(3) Thus the rainfall plays a greater part in producing high fen water levels than the Upware locks.

(4) The fewer dykes are kept open, the wetter the fen will be.

(b) *Observations from May to September*, 1930.

As we have already described (1), the end of May marks the onset of the period of rapid fall of the water table on the fen. This, deduced from the records obtained in one spot only on the fen, the old water-level recorder pit (No. 17), can be seen from our water-level pit data to hold equally well for the fen as a whole. The period recorded in the graphs (Fig. 5) shows the summer behaviour of the water table in a number of pits in different parts of the fen, selected as representing both average and extreme types of behaviour. The unusually heavy rainfall of the end of July, 1930, brought about a rise in the water table all over the fen such as is not usually found in summer: following
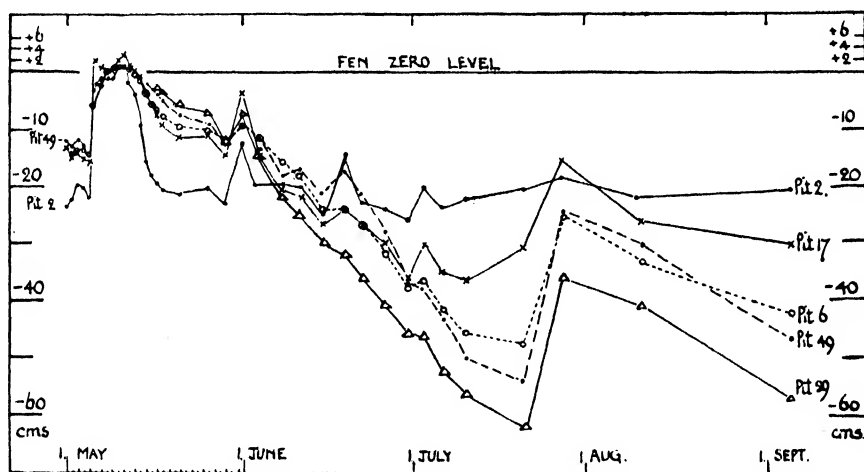
Fig. 5. Diagram to show true relative height of the water table in a series of pits selected from situations in different parts of the fen to show a wide range in their nearness to or distance from drainage channels. The period begins with the abnormally high water-levels of May, 1930, and shows subsequent establishment of typical low summer levels (see text, p. 166). The water table is flattest at periods of high water-level (i.e. the true relative heights coincide most closely).

the drier period at the end of August, however, the typical low levels were again established. The summer fall in level is best shown by pits Nos. 29, 6 and 49 in Fig. 5. By July 20 they showed respectively a water table 62, 54 and 48 cm. below the fen zero level (F.Z.L.). At this time the level in Drainers' Dyke (pit No. 23) was only 17·5 cm. below F.Z.L. All three pits, Nos. 29, 6 and 49, are considerably distant from drainage channels, though they are situated in very different vegetation, No. 6 in a middle-aged carr, and Nos. 29 and 49 in "sedge" or "mixed sedge" of 1 year's growth after the fen fire of 1929. The other extreme of behaviour is shown by pit No. 2, which, as we have already seen, is so close to Drainers' Dyke as to maintain virtually the level of that channel. It is very striking to see how constant the level remains in this

pit throughout the summer, and indeed if we except the short period of May 6 to 10, 1930, when the Upware sluices were closed and the level of the lodes rose in consequence, records throughout the year show little deviation in the level here from an average value of about 20 cm. below F.Z.L. This is further evidence in favour of the conclusion we have already drawn that changes in level of the lode system are only infrequently responsible for any changes of level in the fen itself[1].

Between the extremes indicated lies the record of No. 17, the water-level recorder pit. It is clearly influenced partially by the drainage system, so that on July 20 the water in it was only 30 cm. below F.Z.L. instead of about 50 cm. as in the middle of the fen.

From the water-level data of the fen, graphs of the same type as the five just discussed can be constructed for most of the 70 pits on the fen. If this is done, it is found that according to their position in the fen they behave like No. 2 (lodes and dykes), No. 17 (intermediate), or Nos. 49, 6 and 29 (mid-fen pits); all intermediate types occur, but none lies outside the limits shown except those of the drains themselves and very closely bordering pits such as No. 23. Even these differ little from No. 2.

In contrast with the wide differences in true relative height of the water in these pits in July, it will be seen that at the period of high-water level in May, they all show identical or very closely similar values, which are round about F.Z.L. So high a water table is unusual on the fen, as also is the extraordinary flatness in the water table of the fen, which is indicated by the similarity in height of the water in pits even in extreme types of situation. The general principle is, however, clear—that at periods of high-water level the water table over the fen is flatter than at periods of low level. From this it follows that the water-level recorder will be a safe index to the behaviour of the water table over the rest of the fen during the periods of high-water level.

As a further comment on the interpretation of the curves in Fig. 5 it should be noted that the fall in level from May 10 to June 1 is largely a matter of drainage to the general restored lode level of about 20 cm. below F.Z.L.: the most rapid fall is in No. 2, the dyke, then No. 17, then No. 6, then No. 49 and then No. 29. During the low-level period of July and August the levels in these four pits appear in exactly the reverse order, suggesting that distance from drainage channels is again responsible for the differences between them, as, in a general way, we have already concluded.

[1] *The changing water level in the lodes.* The lodes really repeat in a much modified way the seasonal behaviour of the fen water table as a whole, tending to have high-water levels in winter and low ones in summer. The range of movement is, however, much less than in the fen itself, and the seasonal change is hardly evident at all in years such as 1928 and 1930, though present in a year such as 1929 when prolonged low summer water levels have obtained in the fen. A graph was given in Part I of this paper (1, Fig. 5) to illustrate the changing lode levels in the autumn of 1929 during the transition phase C.

(c) The yearly drift.

(1) *Discussion.*

In the last section we have referred to the yearly drift of the height of the fen water table, but the observations were limited to the end of phase A (control by rainfall and locks of drainage system) and to phase B (reduction of water level by heavy transpiration) (1). Simultaneous readings of the level in pits in various parts of the fen have indeed been taken at different times of year, but in no very methodical manner such as was begun in May,
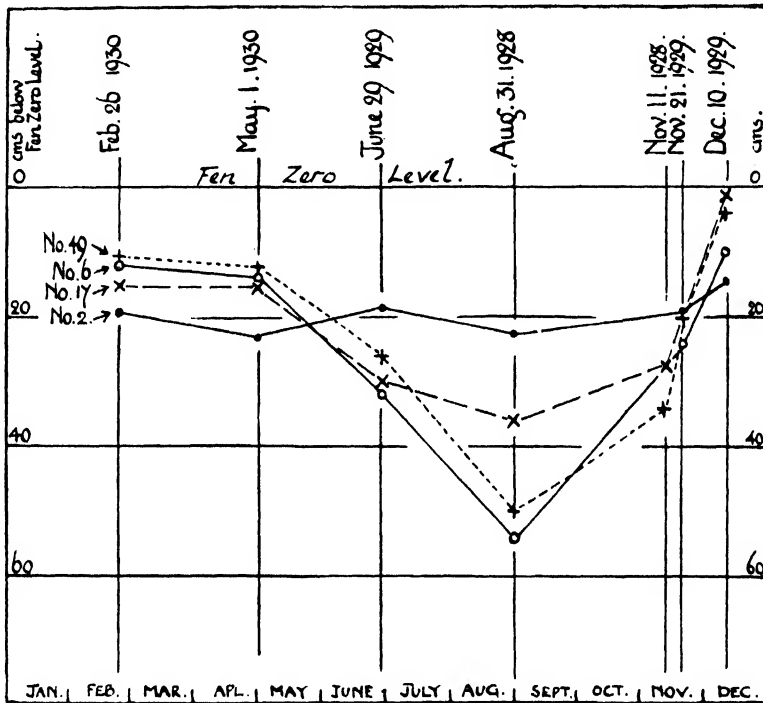
Fig. 6. Diagram to show the true relative height of the water table in four selected pits in different parts of the fen at different times of year (see text).

1930. Readings are available for many different pits on the following dates: August 27, 28, 29, 30, **31**; September 1, 2, 13 of 1928; November 8, 9, 10, **11**, 12, 20 of 1928, June **29**, 1929, November **21**, 1929, December **10**, 1929, February **26**, 1930, May **1**, 1930 and after as already shown. Of these the dates in black type have been selected and the readings plotted in Fig. 6 as if they were all taken in the same year. In this way can be shown in a rough manner the effect of seasonal drift in different parts of the fen. The four pits chosen are the four already used as examples: Nos. 2, 6, 17 and 49. The principles already seen to obtain over shorter periods still hold good for the whole year. Phase A is that of the greatest flatness in the water table, when the true

relative height of the water table is most nearly the same in all the pits. In phase B the curves draw apart and indicate at their maximum separation in August and September the greatest curvature of the water-table surface.
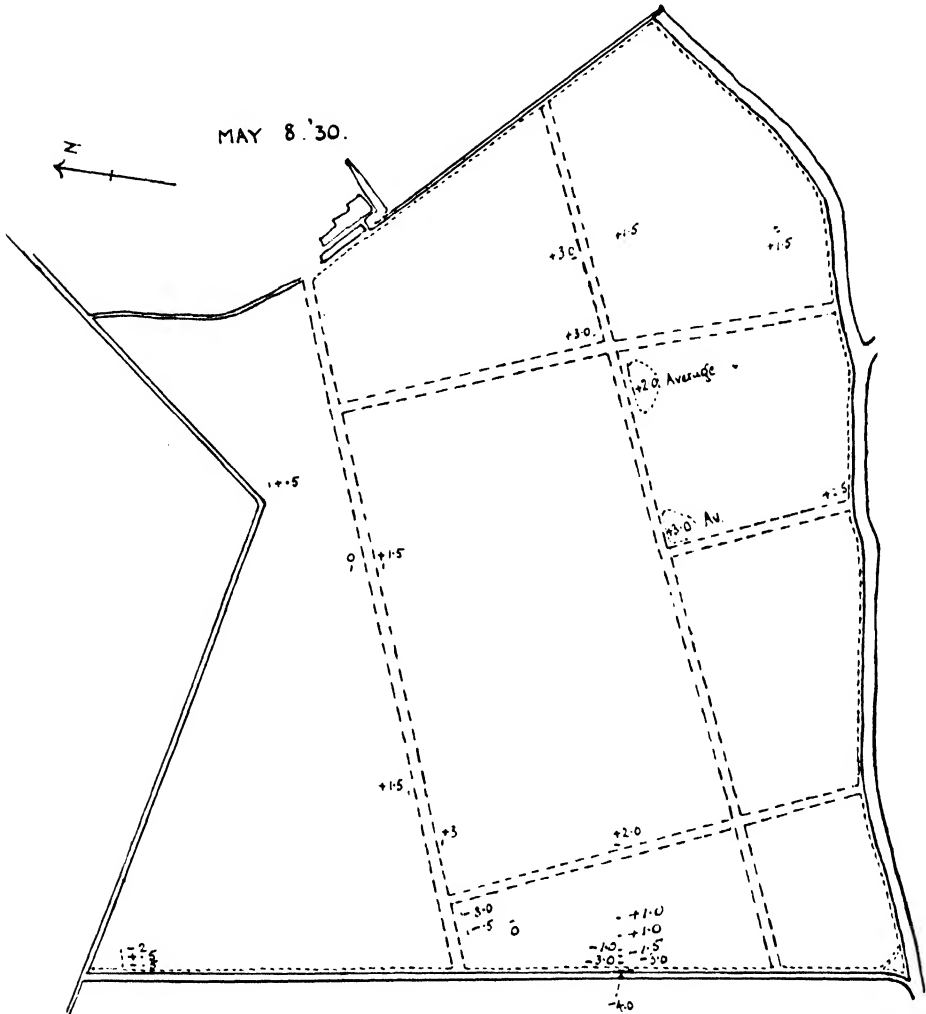
Fig. 7. Map of the fen showing true relative height of the water table in different parts on the given date.

In phase C (failure of the transpiration and filling up by autumn rains) the curves close up again, since at higher levels the water table becomes more nearly flat.

The curvature of the fen water table at different times of year can easily be appreciated from the two maps (Figs. 7 and 8) of the fen for May 8, 1930 and July 20, 1930, periods of maximum and of minimum flatness respectively.

In each map is indicated on the site of each pit (or group of pits) the distance in cm. of the water table below F.Z.L. The saucer shape on July 20 is very well marked. The contrast between the marginal shape of the fen water table under varying conditions is shown in Fig. 9, which illustrates readings of the

FIG. 8. Map of the fen showing true relative height of the water table in different parts on the given date.

true relative height in the series of pits beside Drainers' Dyke at periods of high- and low-water level. The curves for July show the shape typical of phase B, while that for May 17 shows the form typical of phase A. The similarity in dyke level is striking (see p. 167).

Whilst dealing with the yearly drift of the behaviour of the water table it is appropriate to comment on the limited range of movement found in the

water levels. During the winter the water level cannot rise very much above a certain level (say about 10 cm. below F.Z.L.) even during continuous rain, because above this level the rain is no longer filling up pore spaces in the peat, but, over large areas of the fen, is forming sheets of open water, where, with rain falling into an open vessel, the rate of rise per unit rainfall is very slow.
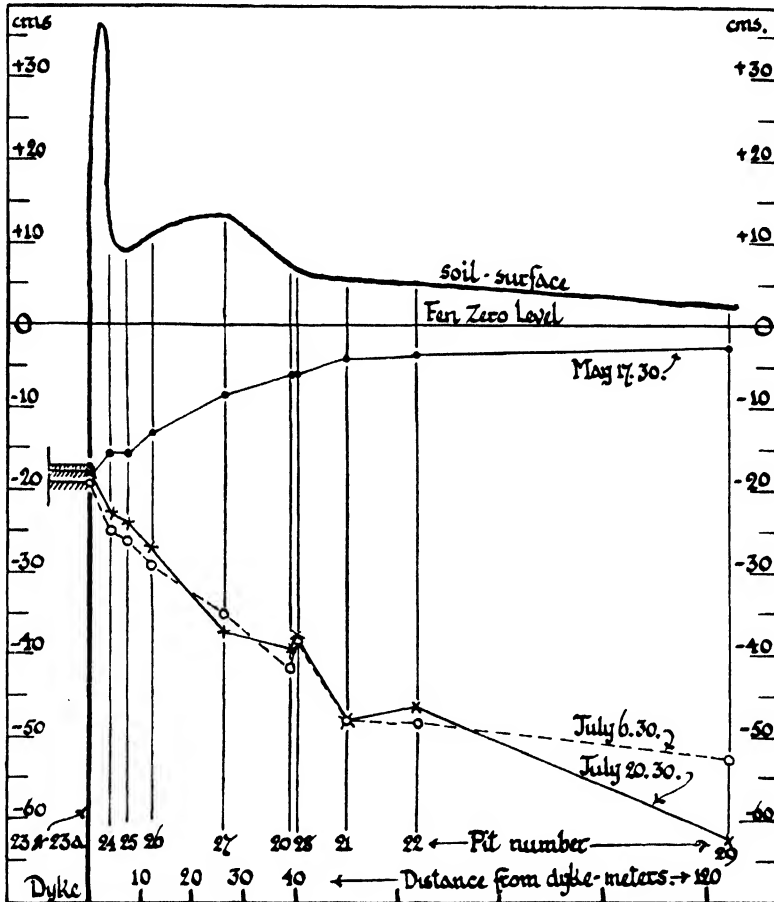
Fig. 9. Diagram to show the true relative height of the water table in the series of pits 20 to 29, near to Drainers' Dyke. The values for May 17 show the shape of water table typical of phase A of the yearly drift, those for July the shape typical of phase B. The dyke level is about the same.

The water level similarly will not fall below the level in the lodes because evaporation and transpiration are at this season negligible. Thus in winter the fen level moves within fairly narrow limits, for lode level is only about 20 cm. below F.Z.L. and if marginal effects are excepted, the fen level as a whole cannot fall much more than 10 cm. below F.Z.L. In summer, of course, the upper limit remains the same, but the lower level often extends to more than 60 cm. below F.Z.L.

(2) Conclusions.

During the periods of high-water level which are maintained constantly throughout phase A of the year (November to May) the fen water table is slightly convex, in shape like an upturned saucer in which the region of marginal curvature is small in area compared with the flat part. The general winter water levels of the middle of the fen lie most frequently about 10 cm. below F.Z.L., and the water levels of the drainage channels themselves are not more than 20 cm. below F.Z.L. Thus even the marginal curvature of the water table is very small, and if we except the drainage channels themselves and the fen within 5 or 10 m. of them we can say that during the winter period of high-water levels the water table of the fen is flat to within 2 or 3 cm. over its whole extent. This is largely attributable, no doubt, to the increased freedom with which water moves about in the fen when the water table is so close to the general surface level, and when it therefore appears as open water in the lower-lying areas. It will be evident that the general level of the water table cannot be increased above a certain amount without corresponding rises in the lode level, and extensive flooding of the fen. Under these conditions, the flatness of the fen water table is, of course, even more marked.

During periods of general low-water level such as occur for a varying length of time in phase B (June to September) of each year, the shape of the water table is concave. At this time its shape is that of a saucer right way up. The saucer rims are the lodes which are about 20 cm. below F.Z.L., and the centre of the saucer is the water table of the middle of the fen, which lies from 40 to 80 cm. or more below F.Z.L., according to the rainfall and transpiration conditions of any given year. The curved margins of the saucer shape are the regions bordering lodes and dykes, from which water is at these times constantly flowing into the middle of the fen. The effects of this marginal curvature are not markedly evident more than 50 m. from the open drainage channels. That part of the water table lying below the middle of the fen, though corresponding in a general way to the middle of the saucer, is not very flat, and shows variations of as much as 20 cm. from one place to another. It is difficult to account accurately for these variations, but we may suggest that they could be due either to unequal rates of water uptake by different types of vegetation or to disguised marginal effects due to obscured or underground drainage systems. It seems clear that their existence indicates less freedom of lateral water movement about the fen at depths of 50 cm. or so below the peat surface than at depths of 10 or 20 cm., such as prevail during the winter.

(d) The automatic recorder as index to the rest of the fen.

Since a continuous record has been obtained for $2\frac{1}{2}$ years of the water level in pit No. 17, it is clearly desirable to know how far movements in that pit represent those in the rest of the fen. We can here summarise the conclusions reached.

Pit No. 17 is of an intermediate character, in that it is mildly affected by proximity to an open drainage channel. It therefore tends to show a more rapid fall after heavy rainfall than the mid-fen pits, and a less rapid fall than marginal pits. The rise due to rain takes place, of course, at the same time in all. It shows a higher summer water table than the mid-fen pits and a lower one than the marginal pits. In summer, during periods of low-water level, because the surface of the water table is then least flat, the water-level recorder pit is of least value as an index to the true relative height of the water table elsewhere on the fen. At other times, when the water table is high (that is, between 0 and 20 cm. below F.Z.L.), the value in pit No. 17 can be taken as an index correct to within a few centimetres of the true relative height of the water table elsewhere on the fen; this follows from the general flatness of the water table at this time.

These considerations readily explain the relations between the two records shown from June 26 onwards in Fig. 10, which gives the complete readings for both the permanent and movable recorders for 1930. The dotted line is that from the recorder in pit No. 17, and the continuous line is that from the movable recorder left in pit No. 49. The record is broken in each case about July 22, when sudden very heavy rainfall made adjustment necessary to both recorders, and this could not be given until July 30. During the heavy transpiration of June and July, with no rain save on July 1, the level fell rapidly in both pits (note the daily periodicity due to transpiration). However, it clearly fell much faster and farther in pit No. 49, and this is almost certainly due largely, if not wholly, to the continual drainage of water into the fen round pit No. 17 from Drainers' Dyke. (Note that at night the level in pit No. 49 is stable, but in No. 17 it shows a strong rise.) After the heavy rain on July 1 and during the intermittent August rains (note the repeated sudden rises) the water level remained between 20 and 30 cm. below F.Z.L., and during this time the two curves behaved in very much the same way, indicating only a fairly constant difference of 2 or 3 cm. In the following rainless period up to September 7 the level in the mid-fen pit sank to 47 cm. as against 31 cm. in pit No. 17. In late September after rainfall, both pits show closely similar levels between 10 and 20 cm. from F.Z.L. This correspondence in levels is even more marked in November and December when the values are between F.Z.L. and a level 10 cm. below it. At this time the mid-fen pit sometimes tends to have a level slightly above that of pit No. 49; this is probably due to drainage from pit No. 17 into Drainers' Dyke, where the level will be somewhat lower.

These data all support the assumption that during periods of high-water level the records of the permanent water-level recorder are applicable with little modification to stations over the whole fen.

A further point of interest is shown by the response of the curves to rainfall. It will be seen that when the level is very high, as in November and
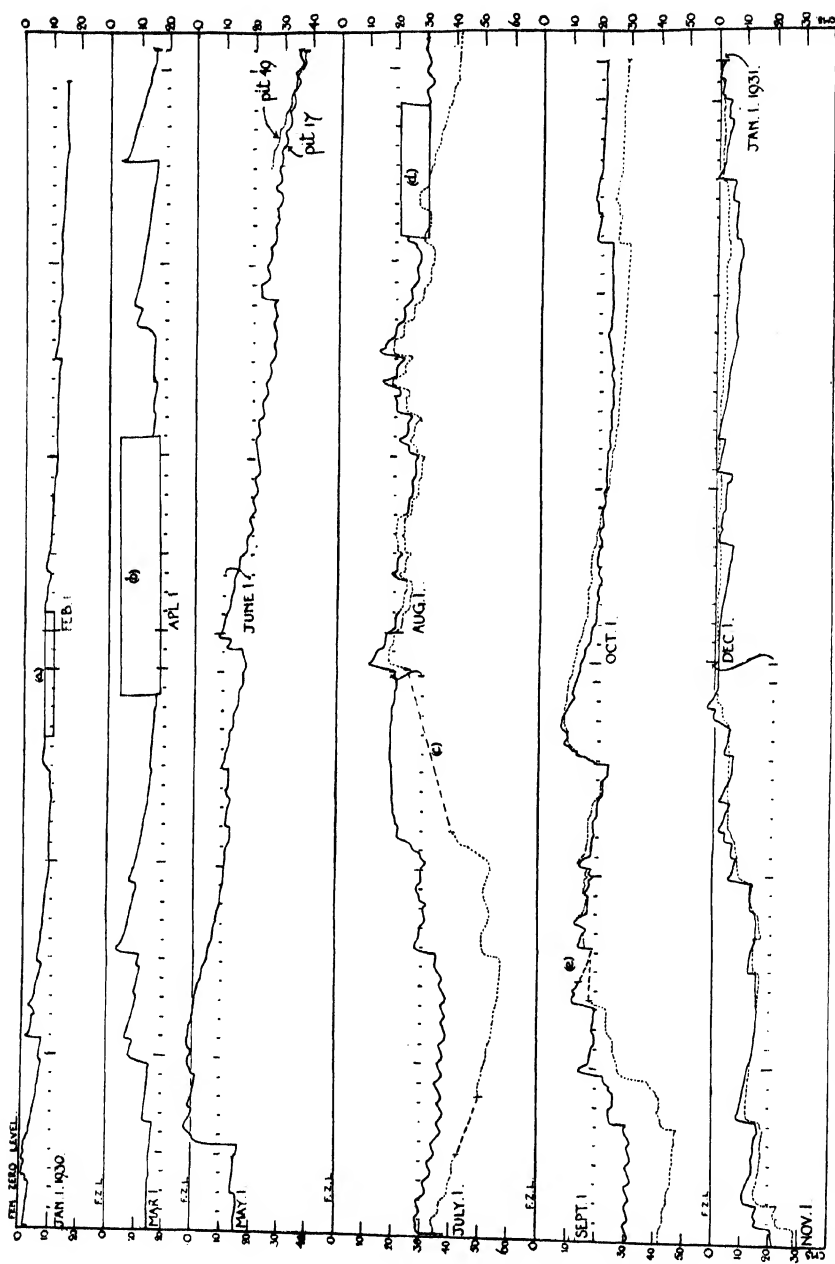
FIG. 10. Diagram to show for 1930 the yearly course of the fen water level given by the two recorders in pits 17 and 49 respectively. The mark shown for each day represents noon. At (*a*), (*b*) and (*d*) there is no record through the clock having run down; the horizontal lines show the extreme limits of water level during this time; it is obtained from the range of travel of the pen on the stationary drum. At (*c*) the broken line shows the probable record.

December, rainfall causes only very slight rise in level in pit No. 49. This is
due to a cause already suggested (p. 171), that at such high levels the rain is
no longer filling pore space in the peat but is forming large areas of open water.
So much is evident by visiting the stations. In the same pit during a period of
lower water level, rainfall produces a rise in level of about 10 times the depth
of rain precipitated. The same is true of pit No. 49 even in November and
December, 1930, because the soil level is there rather above F.Z.L., and at these
times there was no open water formed by the rainfall.

II. CONTROL OF PLANT COMMUNITIES BY THE WATER TABLE.

A. WATER EXCESS AND DEFICIENCY.

The theory of the interrelation of plant communities on the fen has
already been expressed in terms of phases of primary and deflected successions
in the account of fen vegetation given by Godwin and Tansley (2). The
existence of certain of the communities is directly due to different intensities
of "sedge" and "litter" cutting: others are, however, part of the prisere
and are regarded as directly related to increasing height of the soil surface above
the water table of the fen. The stages of the prisere are → reed-swamp → "pure
sedge" → bush colonisation. All the communities which lie on deflected
successions, such as "litter," "sedge," etc., as well as mature carr, must
therefore be regarded as growing on a soil surface even farther raised above
the water table than the driest of these.

In the summer we have already established that under the influence of
high transpiration and drainage inwards from marginal lodes, the water table
in the fen becomes saucer shaped, low in the middle and higher at the edges
and near the open drains. It might well be expected that such a state of
affairs would cause some distinction between the vegetation of the centre and
the edges of the fen, since the plants of the former might be supposed to suffer
from lack of available water during the period of high summer transpiration
far more than those of the latter. Such zonation is indeed present on the fen,
though poorly marked. It is likely that both *Molinia* and the bushes *Rhamnus
catharticus* and *Rhamnus frangula* are more abundant in the marginal belts
round the lodes than elsewhere, and this can be readily seen, for the bushes
at least, in aerial photographs. It is possible, though not perhaps likely,
that this phenomenon is due to differential cutting of bushes in the past,
and without direct measurement of soil level it is not possible to say how
far the true relative heights of the soil level may not be concerned. Apart,
however, from these qualifications, certain definite evidence exists to show
that in most cases on the fen zonation is probably not due to degrees of water
deficiency. This evidence all tends to show that no plant on the fen ever
suffers from lack of available water. In the height of summer in the middle
of the fen, the surface peat below the mattress of dead leaves is always so

moist that it would at once wet the clothes through if one were to sit or kneel on it. At the same time fen plants (seedlings of *Rhamnus frangula*, *Rhamnus catharticus*, *Lythrum salicaria*) growing in cultures in Cambridge and left unwatered in large pots, do not wilt and appear still to grow healthily, without premature yellowing, even when the peat seems quite dry to the touch. It should be said that although they have been looked for, it is difficult if not impossible ever to find plants wilting normally on the fen (i.e. unless broken, etc.). The following figures-show the water content of the fen soil at different times of the year (section A of table).

<div align="center">Table II.</div>

	Date	Vegetation	Depth of sample from soil level (cm.)	Moisture content* (%)	Position of water table in pit 17 (cm.)
A	June 20, 1929	"Litter"	20	564	c. 30
		,,	40	427	
		,,	60	1505	
		,,	80	1836	
	August 3, 1929	Carr	20	449	c. 50
		,,	40	1704	
		,,	60	967	
		,,	80	861	
	February 9, 1929	"Litter"	20	579	c. 15
		Carr	20	579	
	April 11, 1929	"Litter"	20	1383	c. 18
		Carr	20	700	
	March 8, 1929	"Litter"	20	675	c. 24
	May 20, 1929	"Litter"	20	383	c. 20
		,,	40	587	
		,,	80	1000	
B	August, 1930	Seedlings of *R. frangula* kept without water—not yet wilted	Surface soil	43	—
			8–10 (round roots)	95	—
	September, 1930	,,	0–10	112	—
	September, 1930	Barley seedlings kept without water to wilting point (roughly observed)	0–10	29	—

* Expressed as a percentage of the dry weight of the sample.

In section B of the table are given corresponding values for similar fen peat in which plants have been grown either to wilting-point or to a stage just short of this. It seems clear that the water content of the peat of the fen never naturally approaches the values of the wilting coefficient, and indeed seems so far above it that one can hardly suppose that the fen plants ever experience anything but the slightest water deficit.

From such considerations it seems very unlikely that any fen plants ever suffer any important water deficit, and such "xeromorphic" characters as they possess must be explained in terms independent of the existence of xerophytic conditions on the fen of the present day. An alternative explanation for a zonation of vegetation round the fen margin may be given in the re-

latively rapid drainage after rain of the marginal regions, as compared with maintained high-water levels in the middle of the fen. This is naturally a phenomenon of the yearly period of high-water table, and not of the summer, and here it is apparent that control must be held to operate more probably through excess of water than through deficiency.

The situation outlined here offers an interesting parallel to that described by Wells and Shunk (3). These authors established that, in the region investigated, the clear zonation of communities round the bog streams was in all probability directly due to the rates of drainage of the soil at different distances from the streams, and the corresponding periods of time during which the soil lay water-logged after a rise in the water table produced by heavy rain. The plant community least resistant to water-logging occupied the valley centre where there is progressive erosion, and communities more and more resistant occurred in concentric zones outwards.

In Wicken Fen, unfortunately, the zonation is not so well marked, and the relationship is further complicated by human activity in selective cutting of bushes, raising of lode banks, etc. It would not, therefore, be safe to cite this example of zonation as definitely due to these winter-drainage relationships. It is, nevertheless, of the greatest importance in considering the control of the plant communities on the fen by the rising and falling water table to realise that control acts much more probably through excess than through deficiency of water.

B. GRADATION OF PLANT COMMUNITIES.

(a) Preface.

The water-level pits dug in various parts of the fen represent most of the important plant communities. They include (1) reed swamp (Phragmitetum); (2) "pure sedge" (Cladietum); (3) the earliest recognisable stage of colonisation by bushes (especially *Rhamnus frangula* and *R. catharticus*); (4) the young carr (Rhamnetum) characterised by the presence of living *Cladium*; (5) carr devoid of all living *Cladium* (the absence of living *Cladium* marks increasing age of the carr, but it naturally disappears at different times in different cases according to varying initial density of bush spacing, species of bush, etc.); (6) "mixed-sedge," a community dominated by *Cladium mariscus* and *Molinia caerulea* and cut at intervals of 4 or 5 years (see (2)); (7) "litter," a community dominated by *Molinia caerulea*, and cut at intervals of 1 year, now or in the recent past.

The above communities are not all equally represented, as will be seen from the table and figures; for example, little special attention was focused on the Phragmitetum, which is not found at Wicken in such typical development as in many other places; few measurements were made in it. Pits in the "pure sedge" were few in number because of the limited occurrence

of this community on the fen, but the other communities are each represented by several pits distributed as far as possible over the fen.

According to the hypothesis put forward already (2) communities 1, 2, 3, 4 and 5 are stages of the primary hydrarch succession of the fen, and communities 6 and 7 are stages of deflected successions produced by cutting practice of different intensity. Communities 1–5 should therefore occupy situations of increasing dryness and communities 6 and 7 should, according to this hypothesis, occupy places of the same or a greater degree of dryness than communities 3, 4 and 5. Some evidence of this kind has already been put forward (4) as regards a comparison of communities 5, 6 and 7, but much wider data are given here and these provide a much better general test for the hypothesis as a whole.

Readings of the depth of the water table below, or of its height above, the average soil level were taken in all the pits at different times of year. For any given day on which readings have been taken it is thus possible to compare the distance A.S.L. to water level in the various pits. In the figures (11 and 12) the results are given for two representative days only, one a time of high-water level in the fen, December 10, 1929, and the other a period of low-water level, July 10, 1930. Each vertical line represents one pit, and it is shown as if it were on the margin of a fen where the soil surface is sloping down below open water. Thus along the oblique line representing the soil level all the various pits are sorted out, those with A.S.L. below water level to the left, and those with A.S.L. above water level to the right, as in an actual zonation round a lake or marsh. For the sake of clarity, each community from 1 to 7 has its readings placed on a separate oblique line. Fig. 13 shows the true relative heights of the A.S.L. of all the pits in relation to the F.Z.L. At all times of the year when the fen water table is flat, this diagram will indicate the relative height above or below water level of the soil surface in the different pits of the fen. Whichever of the figures we consider, it will be clear that although taken from pits in different parts of the fen, similar plant communities live where the peat surface is of roughly similar height above the water table. In other words the plant communities seem to occupy a range of situations limited in respect of average soil level to water level relationships. It is, however, evident that whilst there is a clear separation between the range of certain communities there is a wide overlap or identity between that of others. These are the relationships we have now to consider, and to facilitate such comparison the data of Figs. 11, 12 and 13 have been summarised in the diagram (Fig. 14).

(b) *Relationship between carr, "mixed sedge" and "litter."*

Whether we consult the July or December diagrams (Fig. 14) it will be quite evident that, as regards the average soil level to water level relationships, there is little to choose between carr on the one hand, represented by
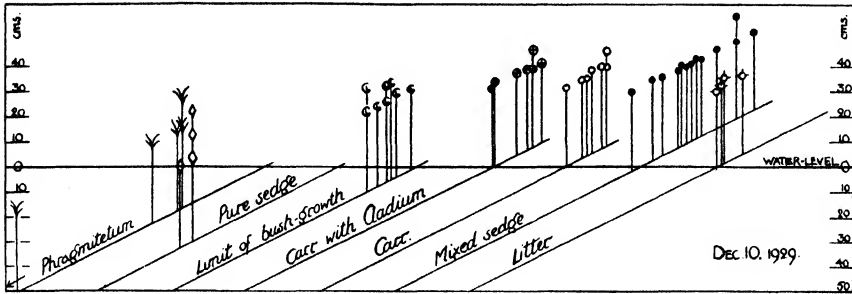
FIG. 11. Diagram to show for December 10, 1929, the distance between average soil level and water level in each of a large number of pits dug in different plant communities and in different parts of the fen. Each vertical line with symbol indicates one pit.
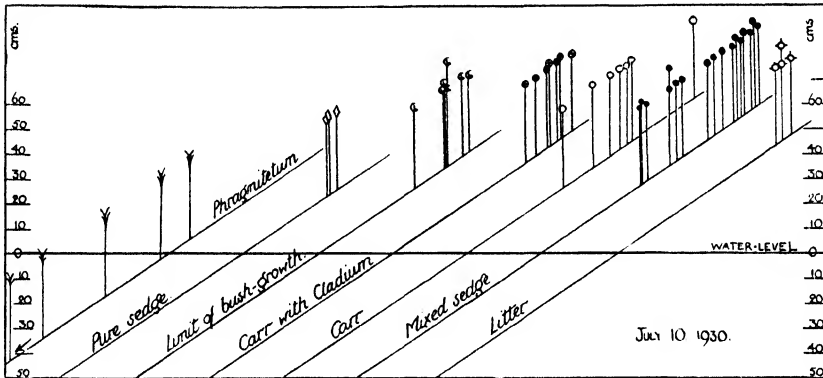
FIG. 12. Diagram to show for July 10, 1930, the distances between average soil level and water level in each of a large number of pits dug in different plant communities in different parts of the fen. Each vertical line with symbol indicates one pit.
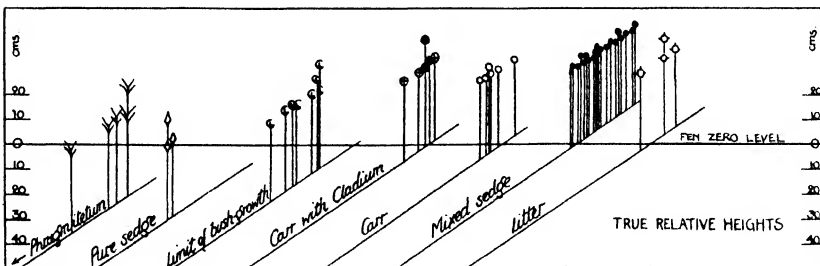
FIG. 13. Diagram to show the true relative height of average soil level (in cm. above or below F.Z.L.) in each of a large number of pits dug in different plant communities and in different parts of the fen. Each vertical line with symbol indicates one pit.

communities 4 and 5, and "mixed sedge" and "litter," communities 6 and 7, on the other. The two latter communities occupy places no wetter and no drier than the two former, save that in the winter diagrams (both December and the true relative height diagram) the "mixed sedge" is found in many parts
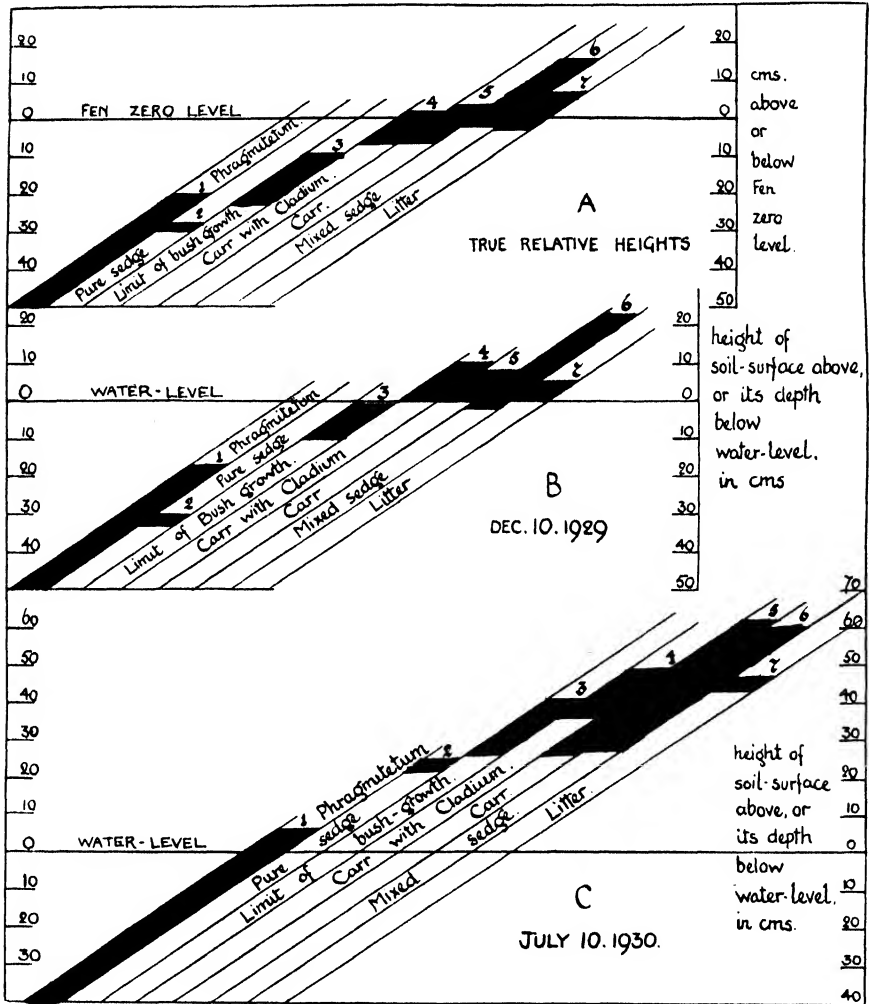
Fig. 14. Diagram summarised from the data of Figs. 11, 12, and 13 to show the range of water-level conditions to which various plant communities in the fen are subject.

of the fen in places much drier than any carr. Under such circumstances, though devoid of bushes, the "mixed sedge" and "litter" could not possibly be regarded as stages in the primary hydrarch fen succession antecedent to carr. The data thus strongly support the hypothesis that "litter" and "mixed sedge" are now kept, or have been kept, free from bushes by repeated crop

cutting, and that despite this peat formation has continued. That is to say, the primary and essential reaction of hydrarch succession, viz. raising of the soil level, has not been inhibited, and the succession has to be regarded as deflected rather than arrested, when such communities are produced.

(c) *Relationship between the limit of bush growth and carr.*

The limit of bush growth is marked on the fen by a series of pits dug in positions carefully chosen as those in which bushes apparently just fail to establish themselves. Their distribution and selection is more fully dealt with in the next section (see p. 184). In most cases within a few decimetres of such pits, but on higher ground, bushes were growing quite successfully.

In a comparison of the true relative height of the soil level here and in carr, it is evident there is no overlap between the two, the carr with and without *Cladium* occupying definitely higher ground. Such data accord exactly with our belief that the limit of bush growth may be accepted as the successional stage prior to bush colonisation and carr formation, and as such it forms a definite critical level suitable for further investigation.

If, however, similar comparison is made by the December and July data, a striking discrepancy between the two becomes evident. In December the same relationship is evident as shown by the true relative heights, a fact due of course to the comparative flatness of the water table in winter. In July, however, we have a very strange state of things. Community 5 and to some extent community 4, both examples of carr, are shown occupying situations fully as wet as those of community 3 (bush limit community), whose wetness prevents any bush development. The distance of soil level above the water table, is, at this time, no greater in many examples of communities 4 and 5 than in those of community 3. The natural occurrence of community 3 was such that the July data seem at first inexplicable. The probable explanation lies in the fact that the control of bush growth by the water table may not be effective at all times of year, and indeed is much more likely, as we have already suggested (p. 175) to operate by excess of water in the high-water level period of the year, than by the deficiency in the period of low-water level. It will be noted that in July the soil level of all the stations in the bush-limit community is at least 25 cm. above the water table, and on December 10 at least 1 cm. below the water table.

We regard the two diagrams of December 10 and July 10 as suggesting very strongly that control of bush growth by the water table is a phenomenon of winter flooding, and further comment along these lines is given in a following section.

A point of further interest in these relationships is the occurrence of "mixed sedge" communities at levels so much above those occupied by any examples of carr (see diagrams of true relative heights). Since all "mixed sedge" is readily colonisable by bushes when left uncut, it seems strange that

no carr should exist in stations as dry as "mixed sedge." Apart from chance, two explanations suggest themselves. One, that areas now bearing "mixed sedge" have been cut for a very long time and their peat level has risen continually, whilst at the same time no "mixed sedge" has gone out of cultivation, and has become colonised by bushes and converted into carr. Two, that although under "mixed sedge" peat formation outbalances peat destruction and shrinkage, yet under carr this may no longer be so, thus causing, through the dominance of the factors causing breakdown of the peat, continual lowering of the soil level.

   If the latter were true, we might expect to find examples of old carr in situations almost as wet as the limit of bush growth, and we might also expect to find, in such carr, bushes in stages of being killed by the high-water table. Such cases are certainly not clearly evident on the fen at the moment, but the process may possibly have been operating for only a short time in any existing carr. The ecological significance of such a process, if present, must be considerable, and must throw into question the probable nature of the final succession of fen carr to the climatic climax of deciduous woodland, if indeed such climatic climax vegetation is to be expected here.

(d) *Relationship between Phragmitetum, "pure sedge" and the bush limit.*

   The communities with which we have already dealt, the bush limit and those of drier ground than this, were the central objects of our water-level investigations, but it seemed advisable to procure simultaneous records of communities in wetter places also if these could easily be obtained. A few pits were therefore made in *Phragmites* reed swamp in one or two fen dykes, and a small group of pits was made in one of the neglected and filled-in dykes of the fen in which *Cladium mariscus* was growing so profusely as to dominate all other plants. These are all that can be obtained on the fen to represent respectively communities 1 and 2, and as they cannot claim to be adequately representative the results need not be discussed at length.

   It is at once apparent, however, in all the diagrams, that both Phragmitetum and "pure sedge" occupy positions of sufficiently lower altitude and wetter nature to be regarded as successive stages in the prisere earlier than the limit of bush growth. The probability that they do represent such stages is increased when we remember the two following points. In the first place the Phragmitetum is here represented in its driest form, as remnants in partly filled-in ditches, whilst on the fen as a whole the bulk of the true reed swamp is found on ground several decimetres lower in level than the examples given here. In the second place, whilst the pits in the "pure sedge" are too few and too close together to be really very significant in themselves, they probably represent the optimal development of a plant community which has its drier limit in what we have called the "bush limit." The vegetation there is certainly dominated only by *Cladium*, though scarcely in the luxuriance with which it

grows in the lower pits. If this is granted, and communities 2 and 3 are merged into one, in the upper part of which comes the limit of bush growth, the data will agree substantially with our view of the general successional relationships of the fen communities. This has been expressed in a second diagram of the true relative height relationships (Fig. 15).

A last point of interest may be made concerning the relationship of the Phragmitetum and the "pure sedge." In the true relative height diagrams and in the December diagram, some overlap is shown between the range of the two communities, whereas in the July diagram they are well spaced out. This might be held to indicate, in parallel with the argument previously used, that the edaphic factor separating the communities was effective in summer rather
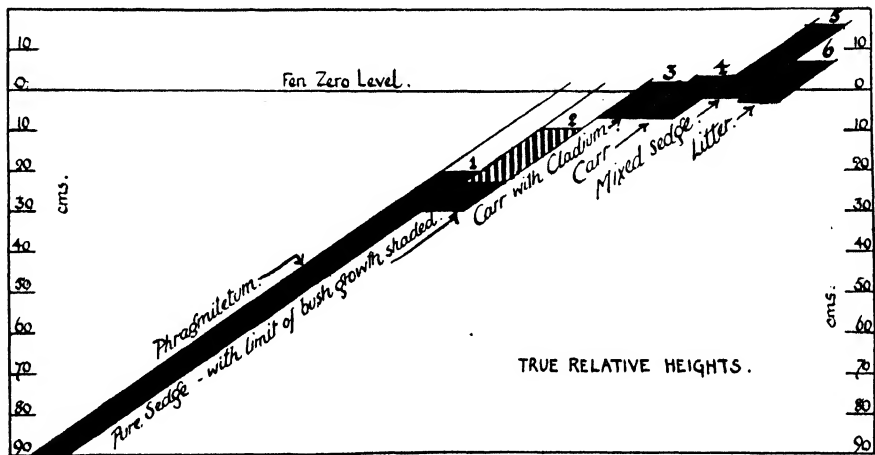
Fig. 15. Diagram expressing the true relative heights of soil level in different fen communities of which 1, 2 and 3 are successional stages of the prisere, and 5 and 6 are phases of deflected successions. 4 can be related both to prisere and to secondary successions.

than in winter. It is, however, probable that the explanation lies rather in an artificial control of the drier Phragmitetum, which in all the pits chosen is cut every year. This is a treatment which rapidly kills out *Cladium*, and is indeed quoted as the general method used in parts of Germany for eradicating it in places where it is a troublesome weed. It has, however, little or no effect on *Phragmites*, for the winter cutting removes only the dead aerial stems of the plant. It may very well be that on this fen *Phragmites* is dominant in the drier ditches solely because cutting has eradicated the *Cladium*, which would otherwise be forming "pure sedge" there. In this case there would be no overlap of the two communities to be considered. At the same time it would not be wise, in view of the sparsity of the data, to reject without further investigation the possibility of summer control differentiating between the two communities.

(e) *Limit of the growth of* Molinia.

An essential component of the "mixed sedge" and "litter" is *Molinia caerulea*: the presence of this plant in considerable amount is the essential factor differentiating "mixed sedge" from "pure sedge." We may therefore regard the wettest examples of "litter" and "mixed sedge" as being close to the lower limit at which *Molinia* will grow. When the average soil level to water level relationships are examined it will be seen how closely the case resembles that of the limit of bush growth. In the diagrams for December and for the true relative height there is no overlap between the range of the "pure sedge" (represented by communities 2 and 3 together) and "mixed sedge" (community 6), but in July there is an overlap of 14 cm. The situation is probably best explained here also in terms of control by the high-water table and absence of control during periods of low-water level.

It is striking to note that the critical level for *Molinia* will, according to this hypothesis, be very close to that of the *Rhamnus* bushes, possibly a little higher; and since *Molinia* cannot grow in the shade of mature carr, it is doubtful whether the plant has any but a very passing occurrence in any phase of the fen prisere. It may even be quite absent from the prisere. If this be true it will owe its very existence on the fen to the cutting cycles maintained there, in the same sort of way as the Agrostido-Festucetum, "grass heath" of the Breck country of East Anglia, has been shown by Farrow to owe its existence entirely to the rabbits which keep it so severely eaten down, but which damage its taller competitors even more.

Under these circumstances all the fen communities containing *Molinia* must be placed in phases of deflected successions or of communities derived in turn from these successions.

(f) *General conclusions.*

The water level and average soil level relationships of different plant communities on the fen bear out the suggestion that Phragmitetum, "pure sedge," and carr are part of the primary hydrarch succession, and "mixed sedge" and "litter" are part of successions deflected from the prisere by crop cutting. The suggested relationship is shown below (Fig. 16); it is the same as that put forward in previous papers (2 and 4).

Further, in regard to bush establishment and the growth of *Molinia*, we may expect control to be effective through the high-water levels in winter, and not in the summer, and the lower limit of growth for the *Rhamnus* bushes and for *Molinia* to be more or less in the same place.

C. Winter water levels at the limit of bush growth.

It has been suggested (p. 175) that control of fen communities in general takes place through excess of water in winter rather than through deficiency in summer, and we have seen special reason to regard the high-water table

during winter as the factor deciding the limit of bush growth on the fen (p. 181). Furthermore, water-level records for 2½ years are available for one part of the fen, and the possibility of extending these results to other parts of the fen has been discussed (p. 173).

It is clearly desirable to formulate at this stage, and as accurately as possible, the nature of the soil level and water level relationships at the limit of bush growth for the past two and a half years. The subject is treated under the following heads: (a) selection of examples, (b) water-level records.
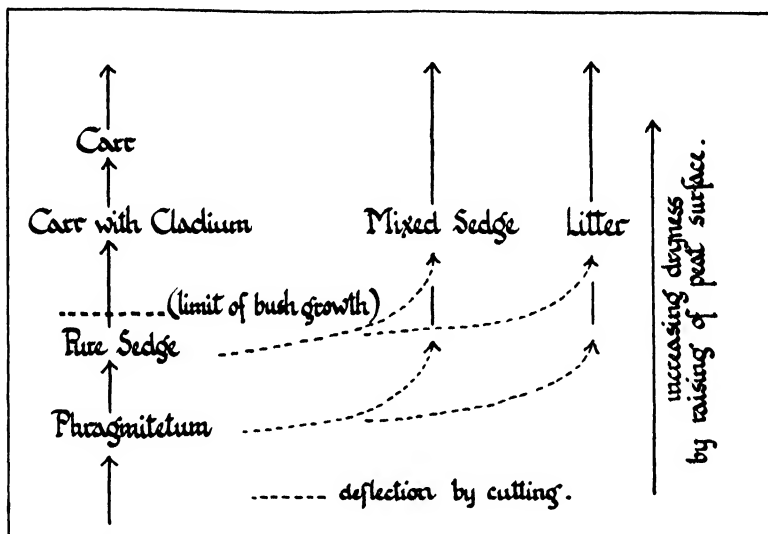
FIG. 16. Diagram to show the successional relations of fen communities. The prisere is on the left. Crop cutting at intervals of 4 or 5 years gives rise to a deflected succession of which "mixed sedge" is part, and cutting at yearly intervals causes a deflected succession in which "litter" occurs.

(a) Selection of examples.

It has been pointed out that bushes are found on Wicken Fen colonising areas of land of very varied heights above the water table, and this has been explained in terms of deflected and secondary successions. Nevertheless, in the prisere of the natural fen vegetation, bushes may be supposed to establish themselves in a sedge community when the peat has reached a fairly definite height above the water table. It proved possible to identify places in the fen which were just too wet for bush establishment and these are spoken of as "the limit of bush growth" or "bush limit." An aerial photograph taken about 1926 showed in a certain area a very conspicuous disposition of bushes in long parallel rows, between which bushes were absent. When visited on the ground, this area was found to consist of ridges and furrows, the result probably of former peat cutting. The ridges were occupied by tall bushes and the furrows by "pure sedge," i.e. a community dominated by *Cladium*

mariscus. On the slopes of the ridges, poorly developed bushes were some-
times growing and it seemed clear that only the lower soil level in the furrows
prevented their colonisation by bushes. Pits were dug close together in the
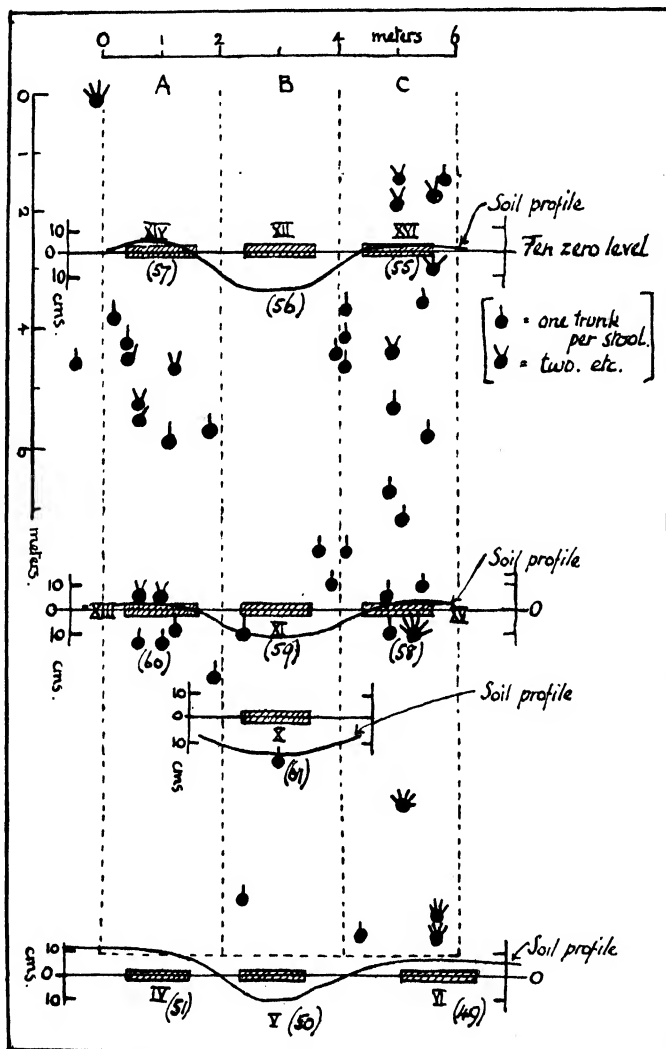
FIG. 17. Diagram to show the disposition of pits and bushes in the ridge and furrow ground,
and to show soil profile. The furrow is regarded as being at the limit of bush growth. The
bracketed figures are the pit numbers.

ridges and furrows of this region, and the nature of their distribution and
that of the bushes is shown in the diagram reproduced (Fig. 17). The pheno-
menon was in fact considerably clearer than can be shown in diagrams of
such small areas, but the general absence of *Rhamnus* bushes from the hollows

is quite clear. The pits were dug originally so as to determine the actual distance between soil level and the water table in each pit, but as the area was so limited in extent and so distant as a whole from drainage channels, the water table was always substantially flat, so that the true relative height of the soil level at each station and the depth of the water table below it in one pit only, would have furnished the same data. As the true relative heights of soil level were subsequently measured for all the pits, we shall refer to them in our discussion.

The pits in the furrows at the limit of bush colonisation were found to have the following true relative heights:

Pit No.	cm.	Pit No.	cm.
53	− 9·5	61	− 16·0
50	− 9·5	59	− 11·5
47	− 10·0	56	− 16·0

In addition to these, a few pits were established scattered about in a similar ridge and furrow area a short distance away from the first, and containing fewer bushes. The true relative heights were:

Pit No.	cm.
45	− 19
63	− 23

It will be seen from these figures that the limit of bush growth is not a simple horizontal plane over the whole fen but a zone several centimetres deep. This is probably due partly to the natural variation in selection of stations to represent the lower limit of bush growth; thus pits Nos. 45 and 63 were probably chosen in places slightly lower than they should have been. A more important cause however is the probability that control of bush distribution by water levels does not give a sharp delimitation. The control may differ in seasons of different water level in the fen and seedlings may establish themselves in dry years in places lower than those colonisable in wet years.

(b) Water-level records.

The true relative height of the average soil level in the recorder pit was + 0·5 cm. in respect to the F.Z.L. From the record it is possible to identify the exact days between March, 1928, and September, 1930, on which the water level near the recorder was at or above the average soil level. It is also possible to state the days on which the water level would have been at or above any given height in the recorder pit. For convenience the positions of 0, 10 and 20 cm. below average soil level have been chosen, that is to say + 0·5, − 9·5 and − 19·5 cm. true relative height. The results for these positions are given in the three columns of the annexed table (Fig. 18). We may express the meanings of the figures in the columns alternatively by saying that they represent the periods of flooding, at or above average soil level, which would have occurred in the recorder pit had the soil level been (a) at its present height, (b) 10 cm. lower, (c) 20 cm. lower.

From what we have said before it can be taken that the results given in this table are applicable in a general way to the part of the fen in which the bush limit pits are situated. This is possible because it is during flooding that

Average soil level (+0.5 cms. T.R.H.)		10 cms below A.S.L. (-9.5 cms. T.R.H.)		20 cms below A.S.L. (-19.5 cms. T.R.H.)	
Date	Days flooded.	Date	Days flooded.	Date	Days flooded.
1928.				Mar. Apl.	} 37
		May June	1,1, .5,1.5,2.	May June	1.5,13, 16,.5,
				Oct. Nov. Dec.	1.5,.5,.5,1.6, 1.7, } >20.
1929.		Jan Feb	} 6.	Jan. Feb.	} 44.
				Mar. Apl.	} <27.
		May	2.	May June	} 15
				July	1.5
			<15.	Oct. Nov. Dec.	.5,3,.5.
Dec. 1930	.5.	Dec.	15.		
		Jan. Feb. Mar.	} 45. 3,5, } ?	Jan. Feb. Mar. Apl. May June	} 210.
May	1,.5,1.5.	Apl. May	1,2.5,13,.5	July Aug.	} 10. .5,1.5.

Fɪɢ. 18. Table showing flooding experience in pit No. 17 (recorder pit) at three given levels, from March, 1928 to August, 1930. In each case the figures for days flooded refer to periods of *continuous* submersion.

the fen water table is most nearly flat, and the deeper the flooding, the flatter will be the water table and the closer the correspondence between the behaviour in different parts of the fen. As a flooding period is usually begun by heavy rains, the commencement of such a period will tend to be about the same in all parts of the fen, and in the high-water levels then produced previous differences

in water level in different parts of the fen will tend to be obliterated. Thus the difference in duration of a flood period in different parts of the fen will depend mainly on the rate of subsequent drainage from them to the lodes and dykes (loss by evaporation having practically negligible effect in winter). We have already seen that the pits Nos. 49, 46, etc., in the bush limit region, drain less well than No. 17, the recorder pit, so that floods will last longer in the former than in the latter. Thus the values in days of continuous flooding given in the table represent *minimum* values when applied to the region of the bush limit pits. Probably each period should be lengthened by a few days. The exact conditions await examination of the results of a recorder left for a considerable time in the bush limit pits themselves.

Keeping the above qualification in mind, however, we may consider the table as an index to the flooding experience at the limits of bush growth.

In the first place, the difference produced by only 10 cm. in vertical height is very striking: thus in the winter of 1929–30, at 0·5 cm. true relative height there was no flooding, whilst at -- 9·5 cm. for no less than 48 consecutive days the water table was at or above soil level. Ten centimetres more in depth produces another very considerable change: it will be seen that at $- 19·5$ cm. from November, 1929, the soil surface was submerged continuously for 210 days.

In the second place, following the data already given, we may provisionally place the bush limit between $- 9·5$ and $- 19·5$ cm. Thus the limit of bush growth seems to be at that soil level which is subject to winter floods of several weeks' duration. This conclusion is in harmony with the previously deduced point that control of bush growth is effective through the winter water levels, for it seems not unreasonable to see, in the flood periods here described, the actual mechanism involved.

Numerous factors necessarily complicate the straightforward development of the solution of the problem from this point. Thus direct evidence has to be obtained that prolonged flooding will kill out *Rhamnus* bushes. Though it is not difficult to suppose that total submergence of many weeks will kill out a small seedling, evidence must be produced of the effect of a water table at, or just above, the soil surface. It must further be recognised that a given length of flooding might have very different effects at different seasons of the year, and one would indeed expect the leafless dormant winter stage, the active leafy summer stage, and the active spring stage of leaf and shoot development, to show very varying susceptibilities.

It must also be remembered that whilst possibly a given flood (say 5 cm. above A.S.L. for 10 days) would kill a 1 year seedling, it might fail to kill a taller, better established seedling of greater age (say 5 years). Thus if for 5 years there were no floods of the given height and duration, seedlings could grow which would not be destroyed by such a flood in the sixth year. Such an effect as this would, as we have said, necessarily modify the clearness of the critical bush level.

It might, of course, prove that not seedlings, but adult bushes were more susceptible to flooding, though this is against the authors' present experience.

A further possible error lies in the unevenness of the soil surface. If a pit were dug at an A.S.L. of − 10 cm. true relative height among *Molinia* tussocks of 10 cm. height, any flood at A.S.L. would practically cover young bush seedlings growing between the tussocks, while those on the tussocks would be 5 cm. or so above water level. If a water table at A.S.L. killed seedlings in such country, a flood to A.S.L. would leave survivors on tussocks. Thus the critical height in such a region would be about 5 cm. above A.S.L. In actual fact, of course, the *Molinia* and bush limits seem more or less the same, and there are no tussocks in the bush limit levels, so that the problem is not likely to arise.

We have spoken of the "killing out" of bushes by the high water table, but it may prove that the effect is by no means sharp, and is expressed in impaired vitality and poorer growth, and as such may be complicated by considerations of competition. This is, however, only an anticipation of difficulties which may not arise. We think that the sharpness of the results may well indicate the direct effect of environment on the survival of *Rhamnus* bushes, and as such they present suitable material for experimental treatment. By subjecting seedlings to controlled flood experience we may hope to complete the reconstruction of the chain of causation between the physiology of these species and the distribution in the field of the important communities which they dominate.

III. SUMMARY.

An account has been given of the methods and results of an investigation of the relationship of soil level to water level in different plant communities in Wicken Fen, England. It has been shown how the water table of the fen is affected throughout the year by the factors of transpiration, rainfall and the fen drainage system, and it has been demonstrated that in summer the water table is low and concave, and in winter high and flat over the whole fen to within a few centimetres.

It has been shown that in all probability control of the distribution of plant communities by the relation of water level to soil level is operative through water excess in winter rather than through degrees of water deficiency in summer. The main plant communities of the fen have therefore been considered and classified in accord with their soil level/water level relations in the period of high water level.

The results of such examination suggest that the Phragmitetum (reed swamp), Cladietum ("pure sedge") and Rhamnetum (carr) of the fen are successive stages of the prisere, whereas the Molinio-Cladietum ("mixed sedge") and Molinietum ("litter") are phases of successions deflected from

the prisere by regular crop cutting at intervals of 1 or 2 years or 4 or 5 years respectively.

Special consideration has been given to the soil level/water level relations of the upper part of the Cladietum ("pure sedge") which has been distinguished as the "limit of bush growth." It is a phase representing the earliest possibility of bush colonisation and is shown in areas just too low and too wet for bush establishment. From continuous water level records through the years 1928, 1929 and 1930, it has been deduced that stations within the zone of the limit of bush growth are liable to be subjected to winter flooding of several weeks' duration. It is suggested that this is probably the factor through which the winter control of bush distribution on the fen may be found to operate.

REFERENCES.

(1) **Godwin, H.** "Studies in the Ecology of Wicken Fen," Part I. This JOURN. **19**, 1931.

(2) **Godwin, H.** and **Tansley, A. G.** "The Vegetation of Wicken Fen." *The Natural History of Wicken Fen*, Part V, 1929.

(3) **Wells, B. W.** and **Shunk, I. V.** "A Southern Upland Grass Sedge Bog." *Bulletin No. 32, North Carolina Agricultural Experiment Station*, 1928.

(4) **Godwin, H.** "The Sedge and Litter of Wicken Fen." This JOURN. **17**, 1929.

THE FORM OF THE OBSERVATIONAL UNIT IN QUANTITATIVE ECOLOGY

By A. R. CLAPHAM.

(Department of Botany, Botanic Garden, Oxford.)

(With one Figure in the Text.)

It has been customary in quantitative ecological work to base estimates of the frequency of species in a homogeneous community on counts made within sample squares or "quadrats." Thus Clements (1) defines the quadrat as "a square area of varying size" and states that the quadrat method, i.e. the listing, counting or charting of the plants within a quadrat, "makes it possible to discover and follow the smallest changes and to recognise the innumerable details of structure" (of the plant community). Tansley and Chipp (2) deal first with quadrat methods in their section on "Methods of Charting Vegetation," and then describe transect methods as of value chiefly in the graphical representation of "zonation and transitions of all kinds, whether static or dynamic." They state also that line transects are "very useful in homogeneous vegetation as a method of recording the composition of the community more quickly carried out than quadrat charting," and instance the work of Foxworthy on tropical rain forest in Malaya. In no case, however, is any method preferred to the quadrat method on the grounds of greater *efficiency*, that is, of giving more information as to the composition of homogeneous vegetation per unit area listed or charted.

A plant community is called homogeneous if sample areas placed at random and small compared with the whole area covered by the community, resemble one another closely in floristic composition, each being highly representative of the community. If a maximum be prescribed for the variability of the sample areas, there will be found a minimum size of sample to satisfy the conditions: areas of smaller size, even if adjacent, may differ very considerably in floristic composition. The reasons for this heterogeneity may conveniently be examined under three heads.

(1) Soil characteristics which affect plant growth cannot be absolutely constant over an area, however small it may be. That this factor of soil heterogeneity is an important one is made abundantly clear in the results of "uniformity trials." These are experiments in which a field, uniformly treated and cropped, is divided into numerous small plots before harvesting, yields being determined for each plot separately. Variations between the plots in yield, and therefore presumably in soil fertility, are always found, and the results may be substantially repeated in successive years.

Now if the development of plants of a single species is so variable from point to point, it is evidently probable that capacity to compete with other species will also be variable: whence it may be concluded that even within a community whose vegetation is homogeneous in the wider sense, the mosaic of different species corresponds to some extent with a mosaic of different intensities of soil-fertility factors.

(2) The plants of many species tend to grow gregariously, either because seed is dropped close to the parent plant, or because of vegetative modes of propagation. Other species occur as solitary individuals. Between the solitary types and those most conspicuously gregarious lies a whole range showing intermediate degrees of gregariousness. There is also a wide range in average density, gregariousness and average density being independent or nearly so.

One may regard the capture of a small patch of soil by an individual plant as depending on its competing power, and this as determined by a number of factors which include (a) the suitability of the habitat for that species, and (b) the "invasion pressure" of that species, i.e. the rate of "bombardment" of the area by seeds, spores, or vegetative propagules. In the neighbourhood of a gregarious plant the invasion pressure is very high and may bring about the capture of comparatively unfavourable patches of soil. But nevertheless, for equal invasion pressures the rate of capture (and of loss) will be determined by the suitability of the habitat, and the effect of the gregarious habit will thus be to enhance that of soil heterogeneity: the species mosaic will merely become coarser, but not essentially different. The coarsening will be most pronounced in the most gregarious types, and will diminish with diminishing gregariousness, until with solitary types the grain of the mosaic depends on the area occupied by an individual plant (see (3) below), and its structure then corresponds most closely with the soil-fertility pattern.

Amongst solitary types there will be some with a high average density; and, at the other extreme, some with a very low average density; and for this reason, or because seed parents are poorly productive, with a very low invasion pressure. This type is of interest, since the probabilities that patches of soil of a given area will contain 0, 1, 2, etc., individuals will conform with the Poisson Series (3), even the most suitable habitats having only a very small chance of being occupied. Here, then, as also with the very rare gregarious types, it becomes evident that the distribution is *random*. It is no less so, however, with types of higher average density, whether solitary or gregarious, for their distribution follows more closely that of soil fertility factors, and this is usually random, as a glance at a fertility contour map will show.

Summing up, there is within the community a whole range of types between those whose distribution depends primarily on the distribution of soil fertility, and those whose distribution depends primarily on the small chance that a seed will fall on a given patch of soil. These extremes—the common gregarious and the rare solitary—are considered separately because different sets of causal

factors are involved; but in all cases the distribution is "random" because the causal factors are exceedingly numerous, more or less independent, and at present highly obscure, though they may ultimately be determinable.

(3) Differences in the average area covered by individual plants of different species is a third factor determining the nature of the species mosaic. Its effect, evidently, is merely to increase the range of coarseness of grain in the mosaic, without altering it fundamentally.

The combined effect of these three factors is, then, to give a point-to-point variability in the floristic composition of the plant community, a variability which is essentially the same as the heterogeneity in yield of an agricultural field crop.

It is recognised by agronomists that in laying out field experiments it is usually better to make the individual plots long and narrow, rather than square. Long narrow plots sample the soil more efficiently than square plots of similar area: if an experimental field is divided into a number of narrow strips the yields from these strips are generally less variable than yields from square plots of similar area. It would seem likely, therefore, in view of the arguments adduced above, that the quadrat is not the most efficient sampling unit for ecological work. A quadrat may lie wholly in one small section of the floristic pattern, while a strip will more probably sample all sections. Thus, within a given area of homogeneous vegetation, and with a given area for each sample, quadrats distributed at random are likely to be more variable than narrow strips. If they are more variable any figure deduced from them, such as an average number of plants of a certain species per unit area, has a larger standard error, and thus there is a loss of information compared with that derived from sample areas which are long and narrow.

In order to establish this point a quadrat with sides 4 metres in length was laid out on the closely grazed turf of fixed sand-dunes near St Fergus, Aberdeen-shire. The area was marked with string, and cross-strings divided it into 256 small squares, each with sides $\frac{1}{4}$ metre in length. Five counts were made within each small square: flowering plants of *Euphrasia kerneri*, and flowering heads of *Prunella vulgaris*, *Thymus serpyllum*, *Bellis perennis*, and *Trifolium repens*. Ease of counting was the chief reason for making this choice.

Now, for each set of counts the data can be analysed in several different ways. Most usefully for our present purpose the counts can be compounded to give totals for strips of 16×1 small squares, and this in two directions at right angles; and totals for square blocks of 4×4 small squares. The areas both of the strips and of the larger squares are then 1 square metre. The totals are given in the plan.

The most satisfactory method of comparing efficiencies is by the use of the variance, defined as the average value of the square of the deviations of individual observations from their mean. It is thus $\dfrac{1}{n} \overset{n}{\underset{1}{S}} (x - \bar{x})^2$, where x is one of n observations $x_1, x_2, \dots x_n$, whose mean is $\bar{x}$; and where $\overset{n}{\underset{1}{S}}$ denotes that n

deviations are summed. This formula applies to the variance as calculated from a complete "population." When, as in the problem in hand, we require to *estimate* the variance in the population, and only have information derived from a few samples, the best estimate can be shown to be

$$\frac{1}{n-1} \cdot \overset{n}{\underset{1}{S}} (x - \bar{x})^2.$$

N ← → S

Grid (each cell listed by species E, P, Th, B, Tr):

	Col 1	Col 2	Col 3	Col 4
E	24	55	66	24
P	15	14	6	3
Th	37	60	1	2
B	3	13	11	30
Tr	5	4	6	11
E	47	67	35	8
P	12	59	11	9
Th	11	10	1	1
B	10	5	10	19
Tr	9	12	10	6
E	52	84	39	14
P	26	87	31	9
Th	6	19	1	0
B	4	4	15	18
Tr	6	4	8	21
E	69	126	21	9
P	56	24	20	2
Th	5	29	3	2
B	4	15	26	25
Tr	0	2	5	11

Side table:

E.	P.	Th.	B.	Tr.
38	13	10	8	5
25	5	15	9	9
62	14	55	28	8
44	6	20	12	4
42	3	4	19	12
50	7	4	14	5
31	38	6	4	7
34	43	9	7	13
51	45	5	6	5
58	24	7	4	5
30	44	6	14	17
50	40	8	17	12
46	17	6	13	6
50	35	5	15	3
45	20	16	26	2
74	30	12	16	7

Bottom table:

E.	35	21	52	84	64	85	88	85	62	67	16	16	11	14	11	19
P.	17	45	31	16	33	56	38	57	32	22	7	7	4	10	6	3
Th.	5	9	20	25	17	37	44	20	2	2	1	1	0	0	1	4
B.	10	2	3	6	3	10	8	16	13	23	13	13	17	11	27	37
Tr.	7	2	10	1	1	5	4	8	5	4	11	11	5	22	13	9

E. = *Euphrasia kerneri*
P. = *Prunella vulgaris*
Th. = *Thymus serpyllum*
B. = *Bellis perennis*
Tr. = *Trifolium repens*

Fig. 1.

It will be seen that the variance is the square of the standard deviation (standard error), and is a measure of the dispersion of the observations and therefore of the value which can be attached to the mean of a number of such observations: the greater the variance the smaller the chance that a further observation will fall within prescribed limits. If comparable observations can be made by two different methods, and if the variance of a single observation made by the first method is twice that of one made by the second method, then, in quantity of information gained, two observations of the first type are equivalent to only one of the second. In other words, to gain the same amount of information from the two methods, twice as much work must be done with the first as with the second method.

The statistical procedure was to deal separately with strips running from north to south, strips running from east to west, and squares. This gave three sets of eighty figures, each set consisting of sixteen counts for five different species. Within each set the sums of squares of deviations of counts about the appropriate species means were calculated, these were added over the five species, and the grand total was divided by 75 (= 5 × 15, the $n - 1$ of the formula for estimating variance)

$$V = \frac{1}{75} \cdot \mathop{S}_{1}^{5 \times 16} (x - \bar{x}_s)^2,$$

where $\bar{x}_s$ = mean count for the species to which the observation x belongs.

There resulted three estimates of variance; for strips in two directions, and for squares. The effect of differences in mean density between the five species was eliminated by this procedure, which is equivalent to an Analysis of Variance (**3**).

The results are shown in the table below.

Unit	Estimate of variance
Strips running N. to S.	123·28
Strips running E. to W.	316·26
Average for strips	219·77
Squares	400·80

The analysis makes it evident that strips sixteen times as long as wide are conspicuously less variable than squares, in the ratio of 220 to 401. In other words, for the same area counted, strips have given almost twice as much information as squares; or, *to secure the same amount of information with squares as with strips, nearly twice as large an area would have to be observed.*

The considerable difference in variability between the two sets of strips is due to the fact that the area was not truly homogeneous, the side towards the south having somewhat longer grass with more *Trifolium* and *Bellis* and less *Euphrasia, Prunella* and *Thymus.* That this is the correct explanation is shown by eliminating that portion of the variance which is due to the difference in average density between the north and south halves. The corrected value for strips running east to west is then 178·92, the corresponding value for squares being 264·59. It is noteworthy that even when strips were least favourably placed (running from east to west) they were nevertheless only three-quarters as variable (316 : 401) as squares, a fact which emphasises strikingly the superior efficiency of the strip.

The data are susceptible of analysis in another way which gives information of interest, since it is possible to calculate totals for strips of 8 × 2 small squares, again giving units 1 square metre in area. As with the longer strips there are two sets, in two directions at right angles. The result of treating these totals in exactly the same way as before is given in the table.

Unit	Estimate of variance
Shorter strips running N. to S.	317·36
Shorter strips running E. to W.	379·93
Average	348·65

Three points emerge from these results: firstly, that even these shorter strips, only four times as long as wide, are less variable than squares in the ratio of 349 to 401; secondly, that they are considerably more variable than the longer strips, in the ratio of 349 to 220; thirdly, that the effect of orientation is now less marked, as might be expected.

It is not evident that the theoretical efficiency must reach a maximum value as the strip becomes narrower. It is evident, however, that edge errors, arising from the difficulty of deciding whether a plant does or does not fall within the area, become increasingly important as the width decreases, and there are, therefore, optimum dimensions in practice. These will depend on the nature of the vegetation to be examined, the optimum width being greater for large and spreading than for small and erect plant types. Further investigation of this point is needed and will be undertaken, but it is suggested tentatively that a strip 4 metres by $\frac{1}{4}$ metre is likely to be the most satisfactory substitute for the metre quadrat.

It should be noted that what has been demonstrated for counting is evidently true also for charting and listing.

The use of a narrow strip rather than a square carries with it certain incidental advantages, particularly in facilitating subdivision of the area and in obviating the necessity for trampling on one part while another part is being examined. Care must be taken, of course, that a long strip lies wholly within the homogeneous community about which information is required.

SUMMARY.

It is shown that the quadrat is not the most efficient observational unit for counting, listing or charting homogeneous vegetation, and it is suggested that a rectangular strip 4 metres by $\frac{1}{4}$ metre should replace the quadrat in ecological investigations.

REFERENCES.

(1) **Clements, F. E.** *Plant Physiology and Ecology*, 1907.
(2) **Tansley, A. G.** and **Chipp, T. F.** *Aims and Methods in the Study of Vegetation.* London, 1926.
(3) **Fisher, R. A.** *Statistical Methods for Research Workers.* 3rd Edition. Edinburgh, 1930.

NOMENCLATURE IN ECOLOGICAL PAPERS

TAXONOMY enters largely into the study of ecology, so that it is essential that plants should be correctly identified as otherwise false conclusions are inevitable. But it is not generally realised that the value of proper identification is lost if the names used are in any way ambiguous. The name should signify the plant intended and sufficient information should be given to enable the reader of the paper to know precisely what the author had in mind.

With the object of giving greater precision to the use of names in ecological papers a sub-committee, consisting of ecologists and taxonomists, was appointed by the Council of the British Ecological Society and has drawn up the following memorandum which suggests how the taxonomic aspects of ecological investigations can be made both accurate and more generally useful. The Council has approved these recommendations which it is hoped that contributors to the *Journal of Ecology* will follow as far as is practicable.

<div align="right">

E. J. SALISBURY
(Chairman of Nomenclature sub-committee)

</div>

AUGUST, 1931.

A. Publications dealing with plant communities of areas of which a Flora is available, adequate for the precise identification of taxonomic units.

(1) The author should state the Flora (and Edition) which has been used in determining the taxonomic concepts and nomenclature followed in the paper. Where, for any reason, the author departs from the concepts or names used in the Flora, he should state the authority for his use of each name.

(2) In critical genera, or where identification is uncertain, a name should not be used unless material has been determined by a competent authority. To this end suitable specimens should be forwarded to one of the National Herbaria or direct to a specialist elsewhere. The precise acknowledgment of such assistance in identification adds to the value of the paper.

For all groups except the larger fungi and fresh-water algae the most suitable material for identification consists of herbarium specimens, which, being preserved, will be available for future reference. The larger fungi should be sent, fresh and carefully packed, direct to a specialist. Fresh-water algae should be preserved in 1–2 per cent. formaldehyde.

(3) Where plants, even if of common or well-known species, are of special interest (for instance if they extend the known range, or are peculiar habitat forms, putative hybrids, etc.) specimens should be preserved, preferably in a National Herbarium.

B. *Publications dealing with plant communities in areas of which no Flora adequate for precise identification is available.*

(1) Material of all the taxonomic units, from each community described, and sufficient for subsequent taxonomic study, should be preserved. The specimens should be accompanied by data which will enable them to be correlated with the names given in the paper (e.g. by numbers).

(2) It is desirable that one set of specimens should be deposited in a public Herbarium in the country of their origin. It would be greatly to the advantage of both taxonomy and ecology, and also add to the value of the ecological study itself, if duplicate sets were also deposited in one or more National Herbaria in Europe and/or North America.

(3) The author should indicate the precise significance in which the names are used in the paper, i.e. by citation (*a*) of original or other descriptions used in identification, or (*b*) of type or other authenticated specimens with which the material has been compared. This work can be carried out efficiently only in large and well-equipped herbaria. If, therefore, the author is not himself a taxonomist he will necessarily rely on the assistance of a trained systematist.

For the sake of clarity and convenience, this taxonomic work, especially when involving the description of new species, should be dealt with either at the end of the ecological study or, if of considerable extent, in a distinct paper to which reference should be made. Such separate publication should preferably be in a journal in which taxonomic papers normally appear.

(4) When, for any reason, a plant cannot be specifically named, an adequate description of its life form should be furnished.

C. *An author should state the herbarium or herbaria in which his specimens have been deposited.*

COMPETITIVE RELATIONSHIPS BETWEEN CERTAIN SPECIES OF FRESH-WATER TRICLADS

By R. S. A. BEAUCHAMP AND P. ULLYOTT.

Assistant Naturalists at the Laboratory of the Freshwater Biological Association.

(With three Figures in the Text.)

IF the influence of the bionomic environment on some particular species is to be investigated, it is first necessary to know what are the effects produced by changes in the physical environment. Otherwise phenomena which really depend on the physical environment may be wrongly described as bionomic effects.

Similarly, before considering the competitive relationships between different species of Triclads, it is necessary to know the limiting environmental factors for each, when they are *not* in competition with other species. Only in this way can an accurate idea of the extent of the effect of one on the other or others be obtained.

The species whose competitive relationships we have investigated are *Planaria montenegrina* Chickoff[1] with *Pl. gonocephala* Dugès, and *Pl. alpina* Dana with *Polycelis cornuta* Johnson.

The first case of competition which will be described is that of *Pl. montenegrina* with *Pl. gonocephala*. These animals were found in streams and springs in the western part of the Balkan Peninsula, in the district round Lake Ochrida, and in the Sorrento Peninsula in South Italy.

All the streams where the animals occurred were of the highland brook type (Carpenter, 1928 *b*), running swiftly down steeply sloping land. The bionomic environment was similar in all cases, and as it extended into regions where the temperature of the water was high enough to prevent the occurrence of these triclads, it could not therefore constitute a limiting factor. The physical environment, namely hard water flowing over a stony bottom, was also the same. In each stream system there was a gradual temperature increase from the source downwards. This gradient was in most cases uniform since the streams were unshaded.

---

[1] It is assumed in this paper that *Planaria teratophila* Steinmann found in South Italy is the same as *Planaria montenegrina* Chickoff which occurs in the Balkan Peninsula. This assumption appears to be justified, because it is difficult to find any morphological differences, and the ecological relationships are the same in the two ⟨

Before considering *Pl. montenegrina* (= *Pl. teratophila*) and *Pl. gonocephala* in competition, it is necessary first to investigate the effects of temperature on the two species individually when they are not competing with each other.

Pl. montenegrina was found in undisputed possession of a stream near Agerola, on the steep southern side of the Sorrento Peninsula. Numerous springs formed the source of this stream in which the occurrence of the animal in relation to temperature is represented in Fig. 1. This map shows clearly that there is a sharply marked temperature limit at about 16·5° C.

It is interesting to note that the species is not found just above the mill. Here the water flowed through a wide shallow channel exposed to the sun where the rate of flow was less than in the natural stream with consequent heating up of the water.

Pl. montenegrina was present in many springs and streams in the West Balkans. It occurred in springs all of which were rheocrene with temperatures ranging from 6·6 to 14·2° C. Usually *Pl. gonocephala* was found lower down the streams, but in two places no competition was met with, at Piskepat, on the west shore of Lake Ochrida, and near Lin, also on the west shore of the same lake. The upper limiting temperatures in these two cases were 17 and 15·8° C.

It can therefore be said that *Pl. montenegrina* when not in competition with *Pl. gonocephala* has an upper temperature limit of 16–17° C.

Pl. gonocephala was also found in springs and streams in Albania and southern Yugo-Slavia. When *Pl. montenegrina* is absent this species occurs right up to the spring head, where it was found in rheocrene conditions at temperatures of from 8·5 to 16·2° C. It was also present in two places in helocrene springs at temperatures of 18·6 and 19·2° C.

Pl. gonocephala is therefore capable, when not competing with other species, of extending from a region of temperature of over 20° C. to spring heads as cold as those occupied by *Pl. montenegrina*.

Having thus investigated the effect of temperature on each species separately, it is now possible to consider them in competition. They were found in the same stream system in many places in the West Balkans. Fig. 2 is a temperature-distribution map of a typical district (Dardha, near Korça in Albania). *Pl. montenegrina* was in sole possession of the spring heads and the upper parts of the streams, while *Pl. gonocephala* replaced it entirely in the lower parts. The temperature at which this occurred was from 13 to 14° C., and in all cases there was practically no intermixing of the two species.

In a typical stream therefore, conditions are:

From the spring head to 13–14° C. ...   *Pl. montenegrina,*
From 13–14° C. to 21–23° C. ...   ...   *Pl. gonocephala.*
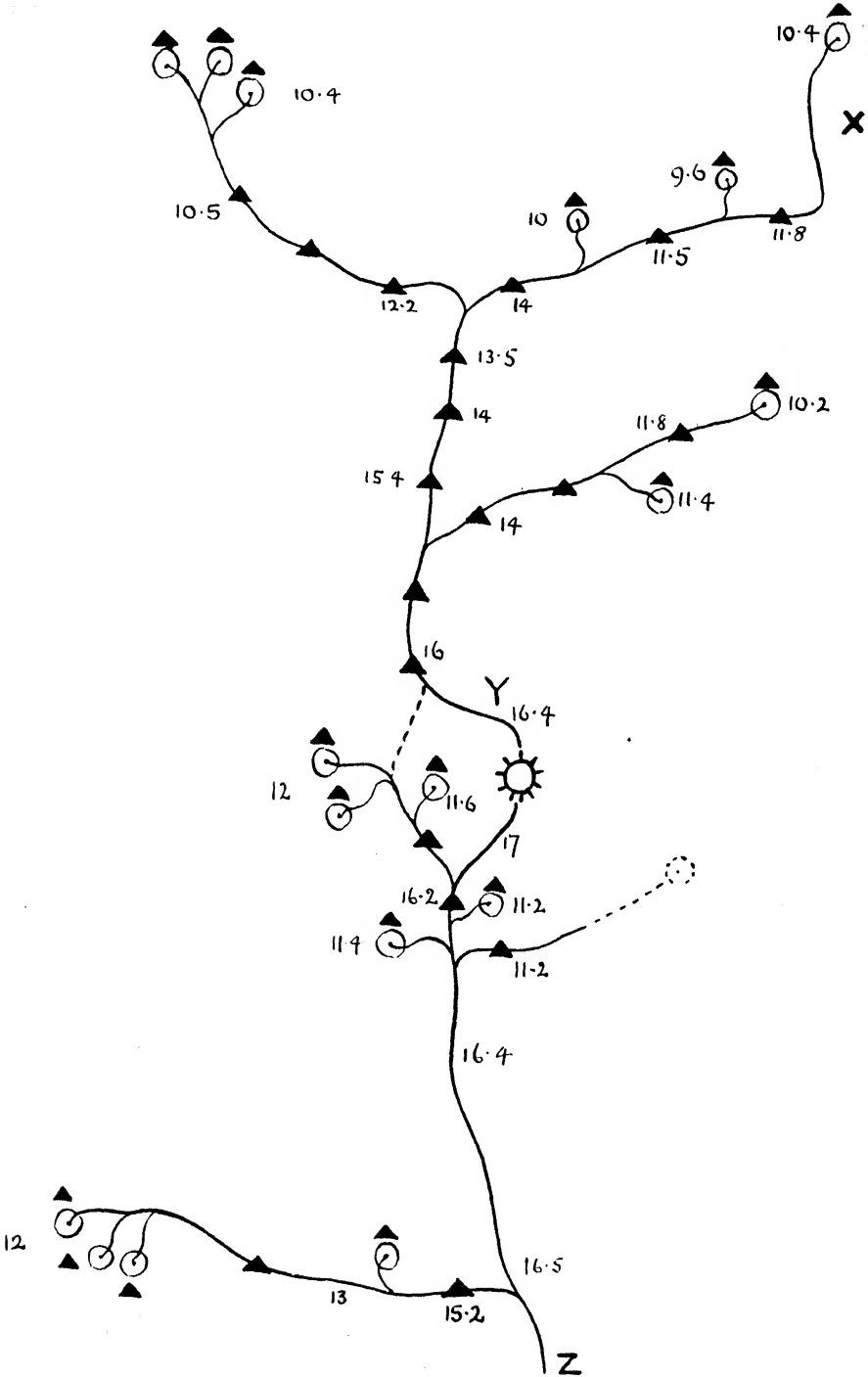
Lower down the stream at temperatures higher than 23° C. there were no planarians.

This limitation of the range of the two species by the presence of each other proves that interspecific competition is occurring; *Pl. montenegrina* is the more successful below 13–14° C., and *Pl. gonocephala* above this temperature.

It is interesting to note that, whereas the presence of *Pl. gonocephala* only limits the range of *Pl. montenegrina* by some 2 or 3° C., *Pl. montenegrina* causes a great limitation in the temperature range over which *Pl. gonocephala* is successful. This factor is of special importance in any consideration of the geographical distribution of the latter species.

The relationships just described are like those which Steinmann (1907), Zschokke (1900), Voigt (1892 and 1904) and others have shown to exist when *Pl. gonocephala* occurs together with *Pl. alpina* and *Pol. cornuta*.

These workers demonstrated that *Pl. alpina* occupies the spring head, and when occurring alone extends down the stream until limited by a temperature of from 14 to 15° C. Under similar conditions *Pol. cornuta* extends as far as 16–17° C., and *Pl. gonocephala* down to 23° C.

Where all three species live in the same stream it was shown that they formed a sequence along the stretch of water. *Pl. alpina* occurred from the spring head till replaced by *Pol. cornuta*, which in turn is supplanted by *Pl. gonocephala*.

The limiting temperature between *Pol. cornuta* and *Pl. gonocephala* is stated by various authors, and their results are in agreement that this occurs at some temperature very close to 15° C. However, when the limiting temperature between *Pl. alpina* and *Pol. cornuta* is quoted there is a much less exact agreement between the values obtained by the various workers. Steinmann gives it as 12° C., whereas Thienemann estimates it as 14·75° C.

The discrepancy in the latter case suggests that, whereas the relationships of *Pl. gonocephala* with *Pol. cornuta* are explicable simply in terms of temperature, the relations existing between *Pol. cornuta* and *Pl. alpina* themselves point to some factor other than temperature having an effect. This idea receives support in the experimental work of Frédéricq (1924), who studied the effect of raising the temperature of the medium in which the three species were kept. Under experimental conditions it was found that *Pl. gonocephala* can withstand a ·temperature of 32° C., while both *Pol. cornuta* and *Pl. alpina* can only tolerate a temperature of 27–28° C. The important point is that there is no de-

Fig. 1. Diagram-map of the distribution of *Pl. montenegrina* in the stream system found at Agerola (South Italy). The spoked circle represents a mill. Circles with dots in the centre represent springs. Black triangles denote the presence of the planarian. The numbers show the temperatures in ° C. At *X* a succession of steep waterfalls is the cause of the absence of *Pl. montenegrina*. At *Y* is the broad shallow channel referred to in the text. Below *Z* the stream was followed further until its temperature had risen to 19° C. At no point were planarians found. The temperatures were all taken during July 1930. The distance between the most distant source and the lowest point on the map was about 5 kilometres.
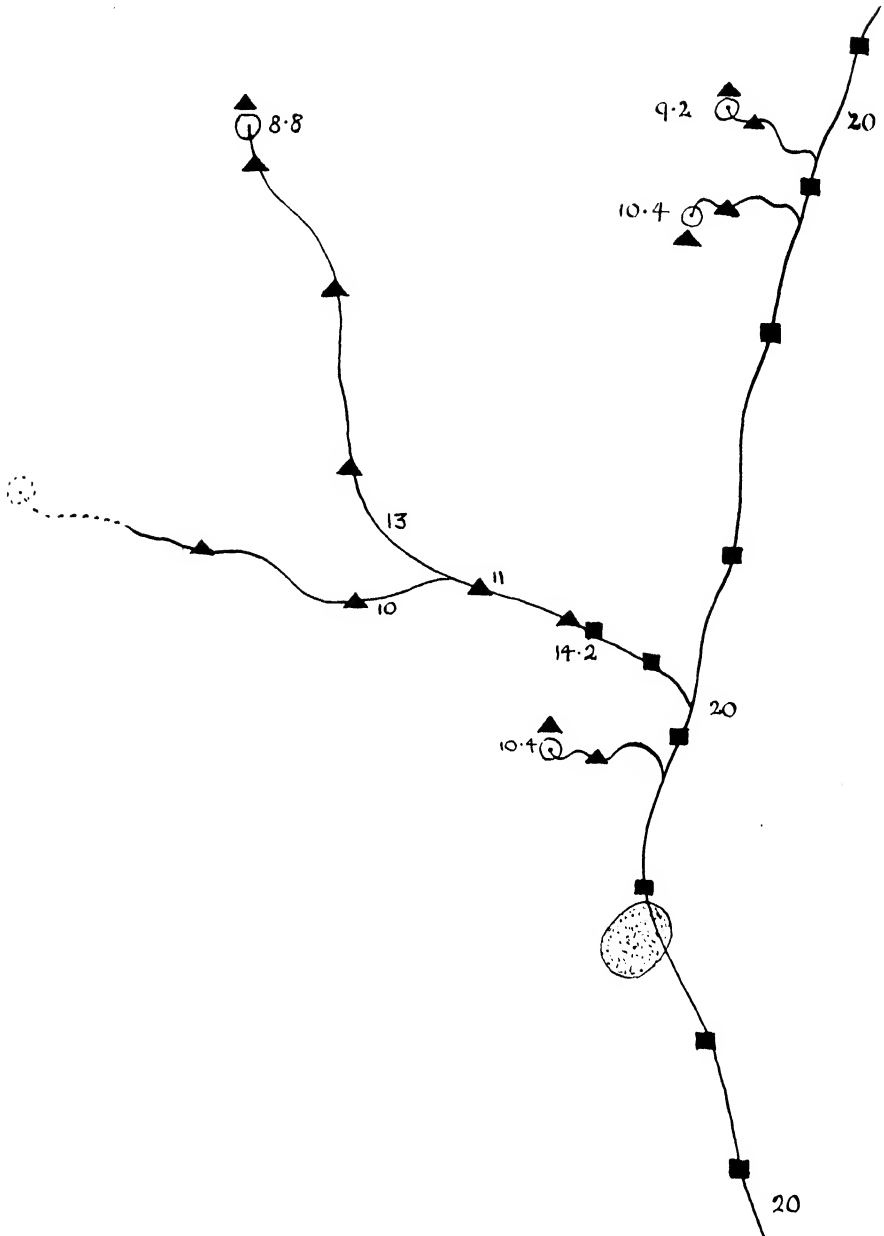
Fig. 2. Diagram-map of the distribution of *Pl. montenegrina* and *Pl. gonocephala* in the stream system at Dardha (near Korça in Albania). The dotted oval area represents the village of Dardha. Circles with dots in the centre represent springs. Black triangles denote the occurrence of *Pl. montenegrina*. Black squares denote the occurrence of *Pl. gonocephala*. The numbers show the temperatures in ° C. All the temperatures were taken during August 1930.

tectable difference in the behaviour of *Pl. alpina* and *Pol. cornuta* towards temperature changes.

In the hope of obtaining information about the factor or factors other than ·temperature which affect the inter-relationships between these last two species, careful investigations of various streams, in which both animals occur, were made. Observations were made on streams in the Lake Maggiore district in North Italy, but the information derived from this source proved to be of far less interest and importance than that obtained recently from a study of the Cotswold area.

It was found that wherever the conditions are uniformly rheocrene a simple limiting temperature relationship exists, with *Pl. alpina* in sole possession of the spring head and extending down to 12·5–13·5° C. After this point *Pl. alpina* is replaced by *Pol. cornuta* which extends downstream as far as 16–17° C. This state of affairs was chiefly met with in North Italy, where the land slopes are much steeper than those of the Cotswolds, with the consequence that the rheocrene character is maintained beyond the temperature limit for *Pol. cornuta*.

In the Cotswolds, cold limnocrene springs are common. Under these conditions *Pol. cornuta* may be in complete possession of the spring head, or at least be present in equal numbers with *Pl. alpina*.

Thus, at Bibury there is a typical limnocrene spring with water welling up in a muddy basin containing numerous pieces of limestone. *Pol. cornuta* is in sole possession of the spring head at a temperature of 10° C., but, a few feet from the source, where the water begins to flow rapidly out of the pool, *Pol. cornuta* and *Pl. alpina* are to be found in equal numbers.

Similar conditions occur at Seven Springs (the source of the Thames) where the pool in which the springs well up is very large. It is interesting to note that in these semi-limnetic surroundings *Pol. nigra* and *Dendrocoelum lacteum* are also to be found at temperatures varying from 9·5 to 10·8° C. in different parts.

A specially interesting and illustrative case was found at Syrford. Fig. 3 is a map of the spring and stream system found there. Waters from two springs, marked *A* and *B*, join the main stream, which flows fairly slowly over a sandy or muddy bottom with scattered stones here and there, and in some places reeds.

In the stream itself, at temperatures below 13° C., *Pl. alpina* and *Pol. cornuta* were found in approximately equal numbers, the latter species, however, appearing to be slightly dominant. There was also a similar relationship between the two species in the spring *B*, which is limnocrene in character and has a level scarcely above that of the main stream, so that the flow is very gentle.

The position of the spring *A* is, however, quite different. It is situated considerably above the main stream and pours water down a steep slope over

which the rate of flow is rapid. *Pl. alpina* is here in exclusive possession of the spring head and that part of the course to the main stream where the water is flowing swiftly down the slope. The two springs, which both have the same temperature (9·5° C.), are situated not more than 20 yards apart.
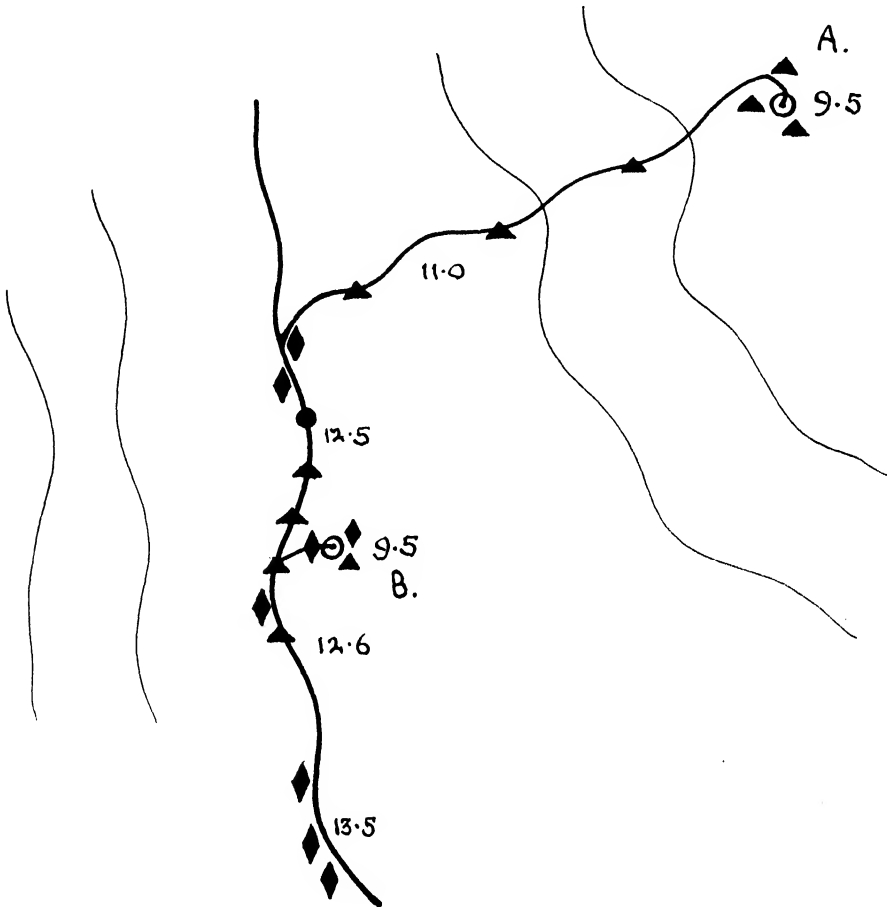
Fig. 3. Diagram-map of the distribution of *Pl. alpina* and *Pol. cornuta* in the stream system at Syrford (in the Cotswolds, England). For description see text. Circles with dots in the centre represent springs. Black triangles denote the occurrence of *Pl. alpina*. Black diamonds denote the occurrence of *Pol. cornuta*. Black circles denote the occurrence of *Pol. nigra*. The numbers show the temperatures in ° C. All temperatures were taken during the early part of September 1930.

From this evidence it is apparent that the rate of flow of the current, as well as the temperature, is a very important factor in determining the success and efficiency of *Pl. alpina* and *Pol. cornuta* when in competition with each other.

In cold rheocrene springs *Pl. alpina* will be in possession of the spring and stream head, while in cold limnocrene springs both *Pl. alpina* and *Pol. cornuta* may either occur in equal numbers, or where there is practically no current until the water overflows the basin in which the spring arises, *Pl. alpina* may be excluded from the basin by *Pol. cornuta* and be found only where the water is flowing away.

SUMMARY.

1. When *Pl. montenegrina* (= *Pl. teratophila*) and *Pl. gonocephala* occur in competition with each other, *temperature* is the factor which governs the relative success and efficiency of the two species. *Pl. montenegrina* is the more successful at temperatures below 13–14° C. Above these temperatures *Pl. gonocephala* is the more efficient form.

2. When *Pl. alpina* is in competition with *Pol. cornuta*, the governing factor is not so much temperature as the *rate of flow* of the water. At temperatures in the neighbourhood of 9° C. *Pl. alpina* is successful in rheocrene conditions, but *Pol. cornuta* dominates in limnocrene conditions.

REFERENCES.

Abraham and **Möldinger.** "Die Tricladenfauna des Tornaer Gebirges." *Zool. Anz.* **86,** 1930.

Bornhauser. "Die Tierwelt der Quellen." *Int. Rev. Hydrobiol.* Biol. Suppt. **5,** 1913.

Bresslau. "Die Verbreitung der Alpenplanarien." *Mitt. d. phil. Ges. in Elsass-Lot.* **5,** 1910.

Carpenter. "Distribution of Turbellarian species in the Aberystwyth district." This JOURN. **16,** 1928 *a.*

Carpenter. *Life in Inland Waters.* London, 1928 *b.*

Frédéricq. "L'autotomie thermique des Planaires d'eau douce." *Acad. roy. Belg. Bull. de la Classe des Sciences,* 1924.

Hankó and **Dudich.** "Ueber das Vorkommen von *Polycelis cornuta* in Ungarn." *Verh. d. Int. Ver. f. Limnol.* 1924.

Krzysik. "*Polycelis cornuta* on the Polish coast." *Odb. z. Spraw. Stac. Hydrobiol. na Wigrach.* 1922.

Stankovič and **Komárek.** "Die Süsswassertricladen des Westbalkans u.s.w." *Zool. Jahrb. Abt. Syst.* **53,** 1927.

Steinmann. "Geographisches und Biologisches von Gebirgsbachplanarien." *Arch. Hydrobiol.* **2,** 1906.

Steinmann. "Die polypharyngeale Planarienformen und ihre Bedeutung für die Dezendenztheorie, Zoographie und Biologie." *Int. Rev. gesamt. Hydrobiol.* **1,** 1908.

Steinmann. "Eine polypharyngeale Planarie von der Umgebung von Neapel." *Zool. Anz.* **32,** 1908.

Steinmann. "Untersuchungen an neuen Tricladen." *Zs. wiss. Zool.* **93,** 1909.

Thienemann. "Die Alpenplanarie am Ostseerand und die Eiszeit." *Zool. Anz.* **29,** 1906.

Thienemann. "Die Faktoren welche die geographische Verbreitung der Süsswasserorganismen regeln." *Arch. Hydrobiol.* **8,** 1913.

Thienemann. "*Polycelis cornuta* in Norddeutschland." *Arch. Hydrobiol.* **13**, 1922.

Voigt. "Die Verbreitung der *Planaria alpina, Planaria gonocephala* und *Polycelis cornuta*." *Sitzb. Niederrhein. Ges. Natur- und Heilkunde,* 1892.

Voigt. "Die Einwanderung der Planarien in unsere Gebirgsbäche." *Verh. Ver. preuss. Rheinl.* **53**, 1896.

Voigt. "Ueber die Wanderungen der Strudelwürmer in unseren Gebirgsbächen." *Verh. Ver. preuss. Rheinl.* **61**, 1904.

Wilhelmi. "Beiträge zur Kenntnis der Verbreitung und Biologie der Süsswassertricladen." *Zool. Anz.* **27**, 1904.

Wilhelmi. "Beiträge zur Oekologie und geographische Verbreitung von *Planaria gonocephala*." *Arch. Hydrobiol.* **13**, 1922.

Zschokke. "Die Tierwelt der Gebirgsbäche." *Ver. Schweiz. naturf. Ges.* 1900.

THE FRESH-WATER BIOLOGICAL LABORATORY ON WINDERMERE, FOUNDED BY THE FRESH-WATER BIOLOGICAL ASSOCIATION OF THE BRITISH EMPIRE

THE laboratory is located in Wray Castle standing about 500 yards from the shore on the west side of the north end of Windermere, and comprises three large rooms adjoining one another and situated on the ground floor. The rooms are completely shut off from the rest of the Castle and the laboratory has its own private entrance. One room is fitted up for microscope work and will accommodate about five workers. Another has been adapted for chemical and physical work and provides accommodation for three workers. Between the two is a smaller preparation room. Under these rooms is a very extensive range of dry cellars, one of which has been converted into an aquarium room. The laboratory is provided with central heating, and a petrol-gas system has been installed, which supplies light and also gas for bunsen burners. There is a good supply of water at considerable pressure.

The Association owns a motor pinnace, 22 ft. long, which, being originally built for the sea, is a sound vessel, suitable for work in even the roughest weather that may be expected on the lake. It is fitted with a Morris Cowley engine with gears, so that the boat can, if desired, be driven at very slow speeds (both forwards and reverse), when towing plankton nets; there is an awning at the stern, with canvas sides giving protection from the weather. A winch driven off the engine and a derrick render this boat suitable for all types of hydrobiological work. In addition a smaller rowing boat is available. The boat-house is about five minutes' walk from the Castle and provides ample accommodation in a covered dock. Above the latter is a room which has been rented by the Association for the storage of gear and nets. A small open dock, beside the boat-house, is available for keeping live specimens in cages. Just outside the Castle is a substantially built conservatory, which will be available for the accommodation of small classes.

The nearest station to Wray Castle is Windermere, 5 miles from Ambleside, which can be reached by a service of buses. Accommodation can be obtained at the Queen's Hotel at Ambleside where, by special arrangement, an inclusive charge of 13s. 6d. per day will be made to workers at the laboratory, except during the summer season (Easter to end of September). Wray Castle is most easily reached from Ambleside by boat across the north end of the lake. There are also occasional buses to Wray. A limited amount of accommodation is also obtainable in this village, which is ten minutes walk from the Castle.

The Youths' Hostels Association have adapted part of the kitchen wing of the Castle as a hostel for their members. Provided there is accommodation

available, visitors to the laboratory may stay in the hostel on payment of the subscription (5s.) to the Youths' Hostels Association and 1s. per night for accommodation. This consists of a bed with bedding in one of the dormitories or in a small room, and the use of the common room, which has a fire. Visitors using the hostel are expected to provide and cook their own meals, but cooking utensils and crockery are available. Visitors to the laboratory, who wish to avail themselves of this accommodation, should write beforehand, stating their needs and the probable duration of their stay, to the Warden, Youths' Hostels Association, Wray Castle, Ambleside.

The staff of the laboratory includes Dr W. H. Pearsall, Reader in Botany in the University of Leeds, who is acting as Honorary Director and visits the station frequently, and two scientific assistants, Mr P. Ullyott and Mr R. S. A. Beauchamp. The accommodation, though limited, is available to members of the Freshwater Biological Association and to other scientific workers desiring to pursue fresh-water biological investigations. The usual charges for using the facilities of the station are two guineas per week for non-members. Members of the Association can make special arrangements by writing to the Honorary Director and stating their requirements.

Workers are expected to bring their own microscopes. A special charge will be made to workers using specially expensive materials or making prolonged use of the motor launch. It is expected that special mention of the facilities provided will be made in published papers dealing with 'researches carried on at the station, and that two separate copies of such researches be supplied to the station. Special terms will be arranged for university and other classes held at the station.

Visitors are not normally allowed in the laboratory without permission. To avoid misunderstanding and disappointment, those who wish to visit, or work in, the laboratory are requested to write to the Director beforehand. All workers will be expected to conform with the rules laid down by the Council for the management of the station. A copy of these rules, as well as any further information required, can be obtained from the Director (**Dr. W. H. Pearsall, Dept. of Botany, The University, Leeds**) to whom all applications for working places should be made.

REVIEWS

CLIMATE AND VEGETATION.

Stefanoff, B. "A parallel classification of climates and vegetation types." *Sbornik Balg. Akad. Nauk.* **26**, 1930. (Bulgarian and German.)

The predominating influence of climate on the distribution of vegetational types has been generally recognised by phytogeographers. Temperature and moisture are the two climatic factors which most directly affect plant life, and not only have the annual means and extremes of temperature, humidity, and precipitation to be considered, but also their seasonal distribution. Stefanoff has made a brave attempt to evolve a scheme of climates which shall enable the phytogeographer to co-ordinate his vegetation types with temperature and general humidity. By means of a quadrat he shows an ideal division of the world's climates into sixteen types. The diagram is reproduced here in black and white (the original is coloured) with translations of the annotations. It is largely self-explanatory. While the climates of large areas of the earth's surface can be placed (metaphorically) in one or other of the sixteen squares, it is certain that many intermediate types occur whose position within the quadrat is more difficult to determine. Moreover, certain important climatic factors do not find expression in the scheme, such as winds and the seasonal relations of high and low temperature with the rainy period.

Criteria for determining and classifying vegetation types are subjected to a useful analysis as a result of which the sixteen climatic types[1] are associated with vegetation, showing peculiarities as follows:

(1) *Cold insular climate.* Closed hygrophytic communities, composed of evergreen microphanerophytes and pseudophanerophytes (chamaephytes of Raunkiaer) of xeromorphic constitution and with buds covered with scales. A short active and a nearly unbroken passive existence.

(2) *Insular climate.* Closed hygrophytic communities, composed of evergreen mega- or mesophanerophytes of xeromorphic constitution, and with scale-covered buds. A rather long-lasting passive and a periodic active existence. The undergrowth and the secondary vegetation composed of hygrophytic pseudophanerophytes with evergreen habit and xeromorphic constitution.

(3) *Warm insular climate.* Closed and mixed hygrophytic communities, composed of evergreen megaphanerophytes with naked buds. Active existence of maximum intensity during the warmest season, which is also the rainy season. The undergrowth and secondary vegetation composed of hygrophytic herbs and shrubs of evergreen habit.

(4) *Tropical rain climate.* Closed and very mixed hygrophytic communities, composed of evergreen megaphanerophytes with naked buds. The epiphytes and the secondary vegetation chiefly formed of hygrophytic phanerophytes and pseudophanerophytes, with evergreen habit and strongly developed aerial root system. Continuous active existence.

(5) *Niveal climate.* Plant covering either absent or composed of scattered microphanerophytes or perennial herbs with a very open and hygrophytic character; at most a short active period of existence.

(6) *Temperate-cold climate.* Closed hygrophytic communities of mixed character, composed especially of summer-green megaphanerophytes (or evergreen conifers) and with scale-covered buds. Periodic active existence with maximum intensity during the summer season. The undergrowth and secondary vegetation composed of hygrophytic summer-green (rarely also evergreen) shrubs and hygrophytic herbs with periodic active existence.

[1] The numbers correspond with those of the squares in the diagram.

(7) *Subtropical climate.* Closed and mixed evergreen communities, composed of xeromorphic phanerophytes, sometimes with reduced leaf surface and naked buds and xerophytic mechanisms. A long-lasting passive existence; the active existence periodic, with minimum intensity during the dry summer season. The undergrowth and the secondary vegetation

POLAR CLIMATE
(TEMPERATURE CONSTANTLY UNDER 0°)

Constant Moisture / Periodic

Rain and Snowfalls 9-12 months, but no persistent snow-covering

Snowfalls 6-9 months with persistent snow-covering

Sparse Snowfalls for 3-6 months with persistent ice-covering

Sparse Snowfalls for 0-3 months without persistent snow-covering

Mean Annual Temperature 0-10°C Absol Minimum below 0°C

Absol Minimum Temperature for 9-12 months below 0°C

INSULAR CLIMATE (WITH CONSTANT MOISTURE)

CONTINENTAL CLIMATE (WITH CONSTANT DROUGHT)

Mean Annual Temperature 0-10°C Absol Minimum up to 0°C

Absol Minimum Temperature for 6-9 months below 0°C

Mean Annual Temperature 10-20°C

Absol Minimum Temperature for 3-6 months below 0°C

Mean Annual Temperature over 20°C

Absol Minimum Temperature for 0-3 months below 0°C.

1 5 9 13
2 6 10 14
3 7 11 15
4 8 12 16

Humid Zone Rain Period 9-12 months

Semi-humid Zone Rain Period 6-9 months

Semi-arid Zone Rain Period 3-6 months

Arid Zone Rain Period 0-3 months or Aperiodic Rain

Under / Over 0°C Absol Min.

EQUATORIAL CLIMATE
(TEMPERATURE CONSTANTLY OVER 20°C)

composed of xerophytic micro- and pseudophanerophytes with evergreen habit and herbs, with periodic winter vegetation (especially of geophytes and therophytes).

(8) *Tropical continental climate.* Half-open or open communities composed of one or a few megaphanerophytes with evergreen or periodically developed leaf system (leaf fall coincides with the dry season). The entire, or only the active, existence periodic, with maximum intensity during the wet summer season. The undergrowth or the secondary vegetation closed or half-closed, composed of xerophytic micro- or pseudophanerophytes with evergreen habit.

(9) *Glacial climate.* The plant covering completely lacking.

(10) *Cold continental climate.* Closed hygrophytic communities composed of one or a few evergreen (Coniferae) or more rarely summer-green megaphanerophytes with protected buds. Almost exclusively periodic existence, of relatively short duration with greatest intensity during the warm season. The undergrowth and secondary vegetation composed of hygrophytic summer-green (rarely also evergreen) shrubs and hygrophytic herbs with periodic summer vegetation.

(11) *Warm continental climate.* Closed pure-wood communities with xerophytic characters composed of few or single megaphanerophytes with winter leaf fall (or Coniferae) and with scale-covered buds. Periodic existence with complete winter rest. The undergrowth and secondary vegetation composed of summer-green shrubs or herbs with periodic development.

(12) *Tropical arid climate.* Half-open mixed communities, composed of typically xerophytic meso- and megaphanerophytes and pseudophanerophytes with evergreen habit and strongly reduced leaf system (Cactaceae, Aizoaceae, Liliaceae, and other succulents). Active periodic vegetation of short duration coinciding with the rainy seasons.

(13) *Cold climate.* Closed and purely hygrophytic communities, composed of hygrophytic herbs and summer-green (more rarely evergreen) microphanerophytes of equal height, with periodic and short duration, with the phase of active life coinciding with the warmest season.

(14) *Continental climate.* Half-closed communities, composed of few especially strongly xerophytic grasses (hemicryptophytes) and summer-green shrubs which have scale-protected buds. The active life phase coincides with the summer season.

(15) *Cold desert climate.* Open communities, composed especially of strongly xerophytic meso- and microphanerophytes and pseudophanerophytes with evergreen habit and strongly reduced leaf surfaces. The secondary element is composed of herbs of short periodic active development, especially of geophytes and therophytes.

(16) *Hot desert climate.* Very open plant covering composed of few or even single much deformed meso- and microphanerophytes with typically xerophytic character and reduced leaf surface. A periodic active vegetation of short duration. The secondary element composed of perennial xerophytic herbs, with evergreen habit, or therophytes and geophytes with very short periodic active phases of existence.

One may express the hope that this paper will be followed by one in which actual climates are classified on the theoretical basis now provided. W. B. TURRILL.

Stojanoff, N. "Versuch einer Analyse des relikten Elements in der Flora der Balkanhalbinsel." (Relict Plants in the Balkan Peninsular Flora.) *Engl. Bot. Jahrb.* **63**, Heft 5, 368. 1930.

The floristic richness of the Balkan Peninsula is well known, as is also the occurrence within its boundaries of many plants whose origins certainly date from pre-Glacial times. The number of these Tertiary relicts is greater than for any other area of equal size in Europe. A study of these plants, of peculiar interest to the phytogeographer, by one who knows so many of them in their natural habitats might be expected to yield data of general value to those engaged in research on plant distribution.

Prof. Stojanoff considers that two extreme groups of relict species can be distinguished: degenerative, as *Haberlea rhodopensis*, and progressive, as *Picea excelsa* (*Picea abies*). He accepts the view that evolution has largely been a process of divergence of forms (Jordanons) from a species (Linneon), the dying out of intermediate forms and continuing divergence leading to the production of new Linneons out of the Jordanons. At the same time a species

shows a rhythmic development and after a certain period of time the number of its individuals and forms becomes reduced. Presumably it is the "species-stock", if such a term may be coined, which throws off Jordanons in its youth[1] and shows signs of senescence after passing its period of optimum vigour. Willis, in his "Age and Area" theory, has neglected the old-age phase of species.

A species at the optimum of its development is often ecologically elastic, i.e. it can adapt itself to different environmental conditions (as to both maritime and continental climates). Many ruderal plants and species with vegetative means of multiplication come under this heading.

Contrasting with these are the regressive species which, having long passed their maximum development, have not only ceased to spread but have a decreasing area of distribution. Mainly as a result of the unequally distributed effects of the Ice Age resulting in relatively denuded ground in Central and North Europe but not in South-east Europe, the former are rich in progressive species while the flora of the latter is noteworthy for the number of regressive relict types. There are, of course, all grades between youthful and senescent species. An additional feature of many of the latter is their taxonomic and phytogeographic isolation and often they have discontinuous areas of distribution. There are areas, of various sizes, where the regressive species are particularly numerous. In these areas it is difficult or impossible to classify the vegetation in detail on the basis of vegetational types, because of the practically infinite number of combinations in which the species occur, as contrasted with progressive species which so often form extensive closed vegetation.

Not all species of Tertiary origin are regressive. Some are ecologically conservative and are at present restricted to a limited area. Thus *Rhododendron ponticum*, *Prunus laurocerasus*, and *Aesculus hippocastanum* need a damp, mild climate. In the Balkan Peninsula they have a very restricted distribution, but in the maritime climate of England they reach a more luxuriant development than in their present native habitats!

In the Diluvial Period of the Balkan Peninsula, with a cool but not extremely cold climate, the relict species obtained refuge in the lowlands and protected valleys. As the large fresh-water lakes, dating from Miocene times, began to dry up, the climate became more continental and a steppe phase predominated. Tertiary types were further restricted to deep, damp, protected gorges of the foot-hills and montane region, especially on limestone, where they are now most abundant in "Tertiary oases." Several such rich botanising grounds are described, including the gorge on the northern face of Červerata Stena (1400 m.) in the Bačkova-Stanimaka district of the northern Rodopes.

In addition to Tertiary oases in which edaphic factors play a conspicuous part, combined with very local climatic conditions, there are other areas in which more extensive climatic zones are suitable for many biologically conservative types. Thus the Strandja Planina of East Bulgaria and Thrace has a very peculiar relict vegetation, some species of which extend farther north and north-west in the Peninsula. The limited distribution of this "South Euxine" vegetation is due in the first place to the unfavourable conditions of the Diluvial Period (more or less coinciding with the "Ice Age"), and in the second to the ecologically conservative nature of the species, limiting them to a comparatively moist climate, which they find on the slopes and in the valleys of the hills bordering the Black Sea.

A rather more puzzling kind of vegetation recalls that of the Asiatic-European steppes. An analysis of the constituent species suggests that they represent an original xerothermic element which has contributed largely to the existing steppe vegetation of East Europe.

A detailed consideration of the distribution of relict species within the Balkan Peninsula enables our author to suggest a division of the whole Peninsula into four "relikten Bezirke": (1) an eastern, including East Thrace, the Strandja district northwards to and including the

---

[1] Our author in quoting *Hieracium* as an example neglects both hybridisation and apomixis.

Dobruja; (2) a central, with the Rodopes, north to the Danube and south to the Aegean Sea; (3) a western, Albania, West Macedonia, and north to the Save; and (4) the Greek, including Epirus, Thessaly, and the Khalkidike Peninsula. It may be pointed out that while Stojanoff criticises Košanin's suggestion of the importance of the Morava-Vardar line for dividing the mountain vegetation of the Balkan Peninsula into eastern and western parts, he uses it as a boundary between his central and western "relict areas."

The history of the beech and pedunculate oak in the Balkan Peninsula and their post-Glacial spread through Europe are considered. The common beech (*Fagus silvatica*) is probably still extending its distribution in the Balkan Peninsula, especially at the expense of coniferous woods, while its older oriental congener (*F. orientalis*) is biologically conservative and therefore limited, in East Bulgaria and Thrace, to the lower moister hills and valleys.

<div align="right">W. B. TURRILL.</div>

LIMNOLOGY.

Naumann, E. *Limnologische Terminologie.* Pp. 776; 158 figs. Price, M. 46.40. Urban and Schwarzenberg, Berlin and Vienna. 1931. (*Abderhalden Handb. d. biol. Arbeitsmethoden*, Abt. IX, Teil 8.)

Every branch of knowledge requires a certain terminology, but among some scientists there is a tendency to overdo the creation of terms, so that they speak in a language which is hardly comprehensible to any but the specialist. This confines the subject to a small group of workers and is specially to be deplored when, as in the case of limnology, it covers a wide field and should therefore appeal to a diversity of interests. One may hope that those responsible for the marked progress in the study of limnology on the Continent will realise the force of this criticism and will desist from the continued creation of new terms. The large number that have been introduced during the last twenty years can be gathered from the dimensions of Naumann's book which is alphabetically arranged in the form of a dictionary and aims at providing a complete glossary of limnological terms. The book does full justice to the wide range of topics covered by the science of limnology; thus, we find not only the more specific hydrobiological terms, but also those referring to the physiography of fresh waters in the widest sense, as well as those employed in fishery, sewage disposal, and the like. Moreover, the majority of the terms introduced by Clements, du Rietz, and others for land vegetation are included.

Naumann's book is, however, far more than a mere glossary, since the brief though comprehensive treatment of numerous topics makes it more of the nature of a condensed encyclopaedia of limnology, which is bound to be of the utmost value as a general reference book. It is impossible to indicate in full the range of topics thus treated in some detail, but the diversity is illustrated by mentioning the articles on flowing waters, the freezing of lakes, high moors, calorimetry of lakes, limonite, pollen analysis, buffer reactions of waters, ponds, peat, supply of potable waters, origin of limnoplankton, dispersal of plankton, etc. Some twenty pages are devoted to limonite, half a dozen to pollen analysis, whilst the consideration of lake types treated from the most diverse points of view occupies upwards of thirty pages. The treatment is lucid, and many of the articles are accompanied by illustrations or diagrams.

It is unfortunate that the author did not see his way to render the book of greater value to the non-German worker. Certain English terms used in relation to sewage disposal, fisheries, etc. are not identical with the German ones, although often only differing in slight details of spelling. Their inclusion, with a statement of the German equivalents, would have occupied little space and would have rendered the book available to a wider public. In general it would seem that the English literature on limnology, scanty as it is, has not received as full a consideration as the continental. Terms like *benthoplankton*, introduced by Griffiths

(this JOURN. **11**, 209), and *consortium,* introduced by the writer (*New Phytol.* **5**, 158, 1906), are not to be found. It is possible that they have been omitted because they have not come into general use, but this objection applies to many of the German terms in the book. The continental literature is fully considered, and in general references are given to standard works embodying the earlier literature. It is not clear, however, why under light absorption no reference is made to the recent work of Oberdorfer (*Zeitschr. f. Bot.* **20**, 465, 1928).

These criticisms, however, refer to minor matters, and there can be no doubt that Naumann is to be congratulated on providing a work of reference which is excellent in its general character and will be indispensable in the library of everyone actively interested in limnology.

F. E. FRITSCH.

SOME RECENT PAPERS ON BRYOPHYTIC AND LICHEN ECOLOGY.

I. **Wiśniewski, T.** "Les associations des Muscinées (Bryophyta) épiphytes de la Pologne, en particulier celles de la forêt vierge de Bialowieźa." *Bulletin International de l'Académie Polonaise des Sciences et des Lettres,* December, 1929.

II. **Kobendza, R.** et **Motyka, J.** "La végétation des éboulis des Monts de Ste Croix." *Bull. Int. Acad. Pol.* July, 1929.

III. **Haugsjå, Pål K.** "Ueber den Einfluss der Stadt Oslo auf die Flechtenvegetation der Bäume. *Nyt Magazin for Naturvidenskaberne,* Bd. **68**, 1930.

The names of plants in these papers do not altogether agree with those used in the British Isles. Where names of bryophytes are quoted the names used are those given in the Census Catalogues of the British Bryological Society. The lichen names are for the most part those given in the British Museum Monographs.

I. The portion of the famous virgin forest of Bialowieźa, in Eastern Poland, which has been studied by the author is that which is now a National Park. It has an area of nearly 5000 ha., and is the most primitive part of the forest, while its trees include all those represented in the forest and its natural condition is specially preserved. Its climate offers conditions exceptionally favourable to the development of bryophytes, the rainfall (500–700 mm.) is greater than in the neighbouring districts, and along the length of the rivers and marshes the atmosphere is relatively saturated. The height above the sea is from 140 to 200 m., the water level is rather high, and there are considerable stretches of wooded swamps.

The richest epiphytic vegetation is found in the Carpinetum, where there is plenty of shade, a high water level and a constant and considerable humidity. In the Alnetum the water level and the humidity are too high for the rich development of epiphytic bryophytes, whilst the Pinetum suffers through the dryness of the soil and the intense insolation. The height at which bryophytes are found on the trees is much lower in the pineries than where other trees are dominant.

The author first discusses the methods used in assessing the frequencies and the concept of association adopted, and then describes various epiphytic associations.

(1) *Anomodon viticulosus* and *Leucodon sciuroides.* Besides these dominant members *Neckera complanata, N. pennata, Homalia trichomanoides, Radula complanata* and *Anomodon longifolius,* are frequent, *Lejeunea cavifolia, Frullania dilatata, Plagiochila asplenioides* and *Metzgeria furcata* are occasional, whilst *Eurhynchium myosuroides, Pylaisia polyantha, Anomodon attenuatus, Leskea polycarpa* and *Dicranum viride* may be considered as rare.

These epiphytes have been noticed up to a height of over 20 m. *Metzgeria furcata* and *Lejeunea cavifolia* rarely occur directly on the bark but on tufts of other bryophytes such as *Leucodon* and *Neckera*. On Carpinus *Leucodon sciuroides* is the dominant bryophyte whilst on the ash and sycamore *Anomodon viticulosus* takes the premier place.

(2) *Hypnum cupressiforme* and *Dicranum montanum*. This association occurs on conifers (*Picea, Pinus, Abies*) and birch, and the greatest height where it was noticed was 3–4 m. *Radula complanata* and *Ptilidium pulcherrimum* are frequent members of the association, *Neckera complanata* and *Metzgeria furcata* may be said to be occasional, whilst *Ulota crispa* var. *crispula, U. bruchii, Neckera pennata, Plagiochila asplenioides, Lepidozia reptans, Frullania dilatata* and *Lejeunea cavifolia* rarely occur.

(3) *Eurhynchium striatum*. This association is not strictly epiphytic but is found at the bases of the trunks. *Mnium undulatum, M. punctatum, Catharinea undulata, Hypnum cupressiforme* and *Plagiothecium silesiacum* are frequent members, *Brachythecium rutabulum, Eurhynchium praelongum* and *Mnium rostratum* are occasional, whilst *Bryum roseum, Thuidium recognitum, Hypnum uncinatum* and *Amblystegium subtile* are rare. In this association the flowering plants *Oxalis acetosella, Geranium robertianum, Lamium galeobdolon* and *Asperula odorata* are often present.

(4) *Hypnum schreberi* in many cases replaces *Eurhynchium striatum* especially at the bases of oaks and spruces. *Hypnum cupressiforme, Hylocomium triquetrum, H. splendens* and *Dicranum scoparium* are frequent, *D. undulatum, Brachythecium rutabulum, Hypnum crista-castrensis, Hylocomium squarrosum* and *Thuidium abietinum* being occasional members. These associations at the bases of the trees are really on the soil.

The obligate relationships of the bryophytes to definite habitats and hosts, their geographical distributions, their biological adaptations in relation to ecological factors are discussed, and the paper is well illustrated by 7 photographs, 13 diagrams of the associations on tree trunks, and 6 maps showing the geographical distributions of *Anomodon attenuatus, Neckera complanata, N. pennata, Hypnum cupressiforme, Radula complanata* and *Metzgeria furcata*.

All these associations are present in the British Isles, though they do not agree in details. The associations of *Eurhynchium striatum* and *Hypnum schreberi* are even less epiphytic with us than Wisniewski considers them to be in Poland. Both these species are definitely terricolous with us, and their subordinate partners, with the exception of *Plagiothecium silesiacum* (one of our rarest mosses), occur chiefly on rocks or earth. We certainly should not expect to find *Thuidium recognitum, T. abietinum* or *Mnium rostratum* in such situations, though *T. tamariscinum* and *M. cuspidatum* would probably be given in our lists. *E. myurum*, which is not given as a member of one of the particularised associations, though it is mentioned elsewhere, frequently covers the bases of our tree trunks. *Leucodon sciuroides* is, as in Poland, almost entirely corticicolous, but its co-dominant, *Anomodon viticulosus*, is usually much nearer to the base of the trunk and in the south-west of England is quite as common on rock or soil as on the tree trunk. Among the subordinates in this association *A. longifolius, A. attenuatus, Plagiochila asplenioides* and *E. myosuroides* are more frequent on soil or rock than on trees, whilst *Leskea polycarpa* seldom occurs except at the bases of trees growing near water. *H. cupressiforme* var. *filiforme* frequently forms large masses on our trees but its Polish co-dominant, *D. montanum*, is a rare plant with us. Among the subordinates *N. pennata* is very rare in Britain, *D. viride* is either absent or overlooked, whilst *Lepidozia reptans* and *Plagiochila asplenioides* are usually on soil or rock. The great similarity of the bryophytes epiphytic on birch and conifers, which is so strikingly shown in Poland, is less evident with us, especially in the southern regions. A certain amount of resemblance both in regard to bryophytes and lichens has been noticed in some of the damp woods of Scotland, e.g. Achrioch wood near Tyndrum, but it is much less evident than that given for the Polish wood.

In the drier woods of Somerset there is very little resemblance and *H. cupressiforme* frequently forms dominating masses on the trunks of angiospermic trees. The attempt to apportion the bryophytic epiphytes to definite trees has been made previously and has met with less success than Wiśniewski has achieved for these Polish woods where the conditions are so humid and constant.

II. The screes of fallen rocks described are those of the Monts de Sainte Croix which are 600 m. high and composed of Cambrian quartzites, grits and schists. The fallen blocks are disposed in three stages: (*A*) 350 m., (*B*) 425 m., (*C*) 550 m. In the first zone there are very few lichens owing to deep shade and great humidity, even *Rhizocarpon geographicum* is absent though *Lecidea contigua* may be plentiful. The second zone has a vegetation more or less intermediate between the first and second. The highest zone, consisting largely of blocks of quartzite of different dimensions, is the most interesting, and is considered in greater detail than the others. *Abies alba* and *Pyrus aucuparia* are the chief trees which occur on the "éboulis" and the vegetative reproduction of these is considered. *Picea excelsa, Acer pseudo-platanus* occasionally occur whilst *Fagus silvatica, Prunus padus* and *Tilia parvifolia* are rare. On the trunks of the beech the mosses *Plagiothecium denticulatum, Hypnum reptile, H. cupressiforme, Dicranum scoparium, D. montanum, Eurhynchium myurum*, the hepatics *Bazzania trilobata, Metzgeria furcata, Lophozia floerkii* and the lichens *Parmelia sulcata, Hypogymnia physodes, Evernia prunastri, Pertusaria pertusa, P. amara* and *Lecidea olivacea* occur. The trunks and branches of the sycamore are more abundantly covered with mosses and hepatics than the same parts of the beech, and this phenomenon is possibly explained by the way in which the bark of the sycamore forms many little chinks, in which the moisture and humus, favourable to the development of bryophytes, can be retained. On *Abies alba* are found *Plagiothecium denticulatum, Hypnum cupressiforme, Ulota crispa* var. *intermedia* and *Lophozia quinquedentata*. It is not particularly surprising that the last named can ascend the base of the tree when one considers the humidity of the locality, but when the authors state that *Hypnum exannulatum* plays a similar rôle a British bryologist is certainly surprised. This is usually a bog plant with us and the trunk of a tree is a very unexpected habitat. The authors, however, make the statement without any qualification or explanation. *Vaccinium myrtillus* plays its usual part on these rock screes. The occurrence and, in part, the special ecology, of *Ribes alpinum, Rubus hirtus, Polypodium vulgare, Lastrea aristata* and *L. spinulosa* are discussed. The mosses *Hypnum cupressiforme, H. schreberi, Hylocomium splendens, Dicranum scoparium, D. undulatum, Webera nutans, Catharinea undulata, Polytrichum juniperum, P. formosum* and the hepatic *Bazzania trilobata* occur between the blocks, the surfaces of which appear to be devoid of vegetation though really covered with lichens. In the places more exposed to the action of sun and wind Cladonietum develops, the most frequent member being *Cladina rangiferina*. The succession is taken as follows. The shaded and wet crevasses between the blocks are occupied by some hepatics (*Lophozia quinquedentata, L. barbata, L. ventricosa, L. floerkii*); then the mosses invade the territory so prepared and finally become the dominant plants. On the humus caught and provided by these, ferns, brambles, briars and whortleberry appear and later some trees. Unless the larger plants find passages between the blocks to the soil beneath they eventually perish. *Pyrus aucuparia* appears to be able to grow for a few years on the humus provided by the mosses but finally succumbs. When the conditions are unfavourable for the development of vascular plants the mosses may give rise to a Cladonietum in the places more exposed to sun and wind. The most frequent member of this Cladonietum is *Cladina rangiferina*, though *C. sylvatica, C. alpestris, Cladonia cornuta, C. gracilis, C. deformis* and others may also occur. When the mossy carpet is more or less shaded and a thick layer of humus has been formed, a different succession follows, if the conditions are sufficiently wet. A Sphagnetum takes the place of the mosses and it is quite possible to find Sphagna such as *S. acutifolium* growing on well-developed, though

somewhat morbid, cushions of *Polytrichum*. This succession is represented by the author as follows

$$Jungermannia \rightarrow Polytrichetum \Big\langle {}^{\textstyle \nearrow\ Sphagnetum}_{\textstyle \searrow\ Cladonietum}$$

Kobendza is responsible for the above account though Motyka is probably responsible for the determination of the lichens mentioned. In the special part contributed by Motyka the Gyrophoretum near the summit is discussed. *Gyrophora polyphylla, G. hyperborea, Parmelia stygia, P. multifida, Hypogymnia encausta* var. *intestiniformis, Pertusaria dealbata* var. *corallina, Lecidea kochiana, L. obscurissima, Cladonia deformis, C. cornuta* and *Cladina alpestris* are present on the north side below the summit of Sainte Croix. The altitude is below 600 m. whereas these lichens, in the nearest localities in which they are found, rarely occur below 1400 m. The conditions are similar to those in the higher regions owing to the exposure of the higher parts of the rocks to the prevalent winds. The lower parts, which have a different association, are protected by snow for a longer time. When the "éboulis" are seen from the west or north-west during summer time they appear almost black owing to the Gyrophorae and Parmeliae. When seen from the east side the colour is yellowish-white owing to the presence of *Rhizocarpon geographicum, Lecidea contigua* and *L. kochiana*. The theory that spores or soredia have been carried from the higher altitudes is considered and rejected because the colonization of suitably exposed rock near to the Gyrophoreta of the Tatras or other neighbouring localities is very tardy and extremely difficult. When a distance of a few metres causes such difficulty, Motyka considers that it is scarcely feasible that the spores or soredia have been carried 200–400 km. and become scattered in situations where development is possible. Then *Parmelia multifida* and *Cladonia cornuta* are the only sorediate members, whilst *G. polyphylla* and *C. alpestris* very rarely produce spores. The great difficulties of this theory of dispersal are avoided if the lichens are considered as relics of the glacial period. The pros and cons of this theory are discussed in a somewhat lengthy manner, though the author does not adopt a too definite attitude on the subject.

The papers are well illustrated by eleven photographs showing various characters of the screes.

III. The influence of the atmospheric conditions of urban districts on the bryophytes and lichens of trees has often been noticed, especially in regard to the sensitiveness of lichens to impure conditions. Crombie, in his *Monograph of British Lichens* published in 1894, states in regard to *Lecanora galactina* var. *dissipata* that it is the only lichen, which, with a state of the type, occurs in the immediate suburbs of London. Frequent references to the sensitiveness of lichens as an indicator of the impurity of the air in industrial districts have been made in lichenological literature, both before and since the time of the reference quoted above. Darbishire said that scarcely any lichen bore apothecia within twenty miles of Manchester and this statement is very near the truth. Even on the Pennines fertile lichens are very scarce since the prevalent winds bring the smoke from the industrial districts, though in a few glens sheltered from such winds some lichens such as *Lecanora polytropa, L. varia, Cladonia pyxidata, Biatora granulosa* and *Verrucaria viridula* are occasionally found bearing apothecia.

Arnold in his *Lichenflora von München* gives many lists of lichens observed on various trees. No article, however, has given such a wealth of detail as the present one, which has 116 pages and 20 maps. The author gives lists and notes on the epiphytic lichens found in 126 stations of 12 districts, shows how great is the influence of atmospheric conditions and what lichens are particularly responsive to such conditions. Details are given of the lichens growing on species of *Acer, Betula, Fraxinus, Populus, Aesculus, Ulmus, Crataegus, Prunus, Tilia, Quercus, Pyrus, Sorbus, Salix, Alnus, Pinus* and *Picea*. The methods by which the factors influence the development of lichens is also considered and 25 lichens are specially

studied. These are *Parmelia scortea, P. sulcata, P. exasperata, P. subaurifera, P. fuliginosa* var. *laetevirens, P. exasperatula, Hypogymnia physodes, Evernia prunastri, Lecanora subfusca, L. hageni, Ramalina farinacea, Xanthoria parietina, X. polycarpa, X. lychnea, X. fallax, Candelaria concolor, Anaptychia ciliaris, Physcia aipolia, P. grisea, P. stellaris, P. tenella* and its form *ascendens, P. pulverulenta, P. tribacia* and *P. virella*. A tabulated list of the occurrence of these in the various stations is given and in this list *Usnea barbata, Parmelia saxatilis, P. caperata, P. olivacea, Hypogymnia physodes* var. *tubulosa, Parmeliopsis ambigua, P. hyperopta, Alectoria jubata, A. sarmentosa, Platysma glaucum, P. chlorophyllum, Ramalina fraxinea, Phlyctis argena, Callopisma aurantiacum, Physcia caesia, Cladonia coccifera Nephromium laevigatum* var. *parile, Lobaria pulmonaria, Lobarina scrobiculata* and *Synechoblastus nigrescens* are also included. The distributions of twenty of the twenty-five special lichens are illustrated by maps. Numerous measurements have been made so as to indicate the percentage area of the tree covered by special lichens. Whether this great amount of labour will be productive of any commensurate result is doubtful, but is a question which can only be answered by a careful analysis of the results and the comparison of similar work in other localities.

Lindsay is quoted on page 75 as giving *Candelaria concolor* as present on stone and Haugsjå rightly considers that some confusion with *Candelariella vitellina* or *Xanthoria lychnea* has occurred. *C. concolor* occasionally occurs on walls, but from Lindsay's remarks in his *Popular History of Lichens* it is evident that he did not discriminate between these three lichens.

W. WATSON.

FOREST ECOLOGY.

Lindquist, Bertil. "Den skandinaviska bokskogens biologi." *Svenska Skogsvårdsföreningens Tidskrift*, Häfte 3, pp. 179–485, 1931, with English summary, "The Ecology of the Scandinavian Beechwoods," pp. 486–520.

Scandinavian literature is rich in works on beech and beechwoods. Inspired by Müller's classic work Scandinavian authors have made a long series of important contributions to our knowledge of the distribution and history of the beech as well as the factors which affect its growth and the floristic cortège of the beech woods. Lindquist's work is the most comprehensive single contribution since Müller's. He deals critically and constructively with the abundant material available, makes substantial additions to our knowledge, but utilises rather than increases what is known about the factors affecting the growth of the beech itself.

The quantitative distribution of the beech in South Sweden is determined by air survey. From a height of 1000 to 3000 m. beech can, during a short period in May, be distinguished from other trees common in South Sweden both by the colour of the young foliage and the date of its appearance, which falls a few days after that of birch and about 10–14 days before oak. It may be suggested that in countries with an oceanic climate and a "halting spring," the actual time during which colour differences can be made out distinctly would be longer, and further that the well-known differences in the date of leafing of individual beeches and races of beeches might present a difficulty in "spotting" isolated trees. For the purpose of mapping Lindquist has, however, found the method quite satisfactory, being detailed and accurate—and the time required was only 30 flying hours.

Three regions are recognised: first, the extreme south of Sweden (along with the whole of Denmark), where spruce as a native tree is absent and beech woods dominate, favoured by a climate with infrequent spring frosts and by the widespread occurrence of calcareous soils; secondly, northwards of this and including the western coastal strip with its extension in

Norway, is the beech-spruce region, where spruce is generally dominant, but beech is distributed throughout the area in small woods or as solitary trees in heaths and in forests of other deciduous trees; thirdly, the "outpost" area north of the beech-spruce region where the beech is sparse. Beech is native in all three regions, but in the beech-spruce region it is now much less abundant owing to exploitation and soil degeneration, and in the outpost area its numbers have fluctuated considerably in historic times, early planting accounting for a pseudo-natural increase and climate and felling for a decrease. As we go northwards from South Sweden the climate becomes progressively less favourable to the beech, climax forest in the south gives way to forest which over considerable areas has retrogressed to heath, and this in turn to the outpost area where beech has a capricious and uncertain tenancy.

The most important climatic factor checking the spread of the beech at its northern limit is the prevalence of spring frosts. The flowering of the beech is periodic and autonomic, but it is influenced by external factors, chiefly by a high temperature during June and July of the previous year. Intensity of heat is more important than duration, and Lindquist considers that this accounts for the tardy migration westwards into an oceanic climate. Successful flowering is not always followed by ripe seed and failure is mainly due to spring frosts which kill the flowers at temperatures between $-1\cdot4$ and $-3°$ C. On the north-eastern limit spring droughts increase the unfavourable effect of the frosts.

The susceptibility of the beech flowers to frost is considered to determine the frequency of the beech and its northern limits in the different climatic periods of post-Glacial time. Thus spring frosts prevented beech occupation of western Sweden and Denmark in Boreal and Atlantic times when beech first appeared in Scandinavia, and continued to limit its spread towards the western seaboards of Denmark and Sweden during the sub-Boreal, although at this time beech entered eastern Denmark and pushed northwards in Sweden. Its absence during this period from Norway and England is held to support this view. It was only with the change to the climate of the sub-Atlantic period, when, the author assumes, there were fewer spring frosts, that the beech was enabled to spread to western Denmark, Norway and England, at the same time withdrawing from its northern outposts in Sweden.

Lindquist attacks the difficult and complicated problem of assessing the influence of light, nitrification and acidity on the occurrence of the chief societies of the ground vegetation of the beech woods. His account, which is not readily amenable to summary treatment, shows how these factors interact and compensate each other within certain limits, outside which any one may be restrictive, and how by a change in one factor others are altered, with resulting important changes in the vegetation. Thus by increasing the light (by thinning the wood) nitrification may be initiated and a limit set to some mycotrophic species (e.g. *Deschampsia flexuosa*) whose fungal symbionts apparently demand conditions restrictive of nitrification.

Correlations would rarely appear to be straightforward and simple, but Lindquist considers that light intensity exercises a controlling influence on the socions of *Oxalis acetosella*, of *Anemone nemorosa*, and of the *Geranium robertianum* group, in which adequate light is necessary to ripen the seeds of the annuals and pseudo-annuals composing it. Too heavy thinning of a wood leads to degeneration of the mull layer and to the dominance of the *Milium effusum*, *Melica uniflora* and *Hordeum europaeum* socions. The maintenance in Swedish forestry practice of adequate thinning to prevent soil degradation is emphasised.

The term nitrification is used as an "expression involving several interdependent processes in the humus layer." Heath species like *Deschampsia flexuosa*, *Vaccinium myrtillus*, *Dryopteris linnaeana*, *Picea excelsa*, flower only where nitrification is absent or proceeding weakly. On the other hand the field layer communities of the "meadow" beech woods are all

primarily or secondarily dependent on nitrification. Three groups are distinguished: (1) *synusiae indifferent to nitrate*, which apparently does not mean that they can exist where nitrate is absent, but only that they are indifferent to the intensity of nitrification. Examples are communities of *Melica uniflora*, *Asperula odorata*, and *Sanicula europaea*. (2) *Facultative nitratophilous synusiae*, which need vigorous nitrification on acid soils (*p*H 5·0–7·0), become more and more dependent on it with increase of acidity and less and less dependent with a decrease. Socions of *Mercurialis perennis*, *Aegopodium podagraria*, *Primula elatior*, *P. vulgaris*, and *Corydalis cava* belong here. (3) *Obligate nitratophilous synusiae* on soils with a *p*H of 4·5–5·5: societies of *Geranium robertianum*, and *Galeopsis tetrahit*, are examples.

Results obtained from cultures to determine the range of acidity tolerated by plants and the application of these in the field are criticised on the ground that in the field quite other factors are really limiting. Communities on raw humus are limited, not by acidity, but by nitrification. In the meadow beech woods three groups are recognised: (1) *synusiae indifferent to acidity*, e.g. socions of *Rubus fruticosus*, *R. idaeus*, *Deschampsia caespitosa*: (2) *acidiphilous synusiae*, confined to very acid or moderately acid soils (acidity greater than *p*H 5·5), e.g. *Milium effusum* socion and (3) *subneutrophilous synusiae* on soils whose acidity is less than *p*H 5·5. Some characteristic subneutrophilous elements are: *Corydalis cava*, *Primula elatior*, *P. vulgaris*, *Mercurialis perennis*, and *Aegopodium podagraria*.

It is but a step to compare the rate of growth of the beech with the ground vegetation. Bornebusch's system of "ground" and "condition" types is taken as a basis, and while no satisfactory correlation can be established with the *Oxalis*, *Oxalis-Anemone* and *Anemone-Asperula* types, yet Lindquist admits that there is a great difference between these and the Mercury and *Corydalis* types; but in summary he concludes that "there is no theoretical basis for the suggestion that the flora types are indicators of the growth, since different factors may have influenced the distribution of flora types on the one hand and tree growth on the other."..."On the other hand a study of the ground flora is of very great importance in its bearing on other subjects, especially on studies of conditions in the humus layer and studies of the conditions for beech reproduction."

It seems desirable to say shortly that Lindquist's criticism of Bornebusch's types would in England apply equally well to his own conclusions regarding the factors determining the occurrence of some of the societies of the forest floor. For example, the dominance of *Oxalis* on the South Downs plateau bears no relation to the light intensity and *Geranium robertianum* is common on alkaline soils of the Chiltern escarpment. Nor do English beech woods lack excellent regeneration on acid soils (*p*H 4·4)—in fact some of the best examples both in England and Scotland are to be found on very acid soils. It may also be remarked that *Pteridium aquilinum*, although not absent from, is certainly not abundant on, basic soils on the Chilterns. All of which simply means that while we may know enough to criticise certain attempts to draw up a system of forest types based on the ground vegetation, evidence against the theory itself is inadequate. Failure to find correlations between the ground vegetation and beech growth may simply mean that we do not yet understand vegetation sufficiently well to interpret it correctly and use it for precise purposes. The *Oxalis* society, for example, is widespread and occurs in widely different forest communities belonging to summer-green deciduous forest and to evergreen coniferous forest. The rate of beech growth in each of these is not necessarily the same, for we are comparing communities which ought not to be compared in that way, and which in time give way to adult communities which are quite different. We fall into the same error as the foresters do when they group together different localities showing the same rate of growth in a tree species planted on them.

Again, to say that the roots tap deeper soil layers than the roots of herbs and to argue therefrom that there can be no correlation between tree growth and vegetation is to make

large assumptions. We do not yet know how far the lower soil layers affect even shallow-rooting plants, and we do not know how much of the tree nutrients comes from the layers occupied by the roots of the herbs and how much from the lower layers. And we have only the most elementary knowledge of the relation between the activities of the roots of different species of trees and the ground vegetation. How far, for example, is the difference in light intensity alone responsible for the fact that similar vegetation is found under much less favourable conditions in oakwood than in beechwood? If the roots of the beech are cut, it may be found that light intensity has little to do with the difference and root activity a great deal. In short we do not yet know enough about vegetation itself and the factors delimiting the ground societies, or about the factors affecting the growth of the beech and the relation between the beech and the ground vegetation, to conclude that ground vegetation is no guide to the potentialities of the habitat.

The paper is the record of an admirable piece of work. It is well illustrated by photographs, graphs, charts and explanatory diagrams and by a large folding map showing the quantitative distribution of the beech forests. The revision of the English summary by Prof. Tansley, Dr and Mrs Godwin, has had the happy result of giving us something which it is a pleasure to read.

A. S. W.

Bourne, Ray. *Regional Survey and its Relation to Stocktaking of the Agricultural and Forest Resources of the British Empire.* Pp. 170, with a folding table and 12 plates from air photographs. Oxford Forestry Memoirs, No. 13, 1931. Clarendon Press. Price 15*s*.

This large memoir is primarily a plea for the need of taking stock of the resources of the Empire in plant communities, whether natural or artificial, and presents a method of carrying this out. This method, called the method of Regional Survey, is tried out across a strip of England from the Oxfordshire-Gloucester boundary to the borders of Berkshire-Surrey. The results occupy the bulk of the memoir.

The plea and general conclusions are given on pp. 7–66, the details in an appendix of about 100 pages. This is an excellent arrangement, for it enables the reader to see the wood without losing himself among the trees.

In the subdivision of land most scientists are agreed on the major units. Up to a certain point geographers, climatologists, ecologists, soil scientists, farmers and foresters walk together; but thereafter they part company, each pursuing his own way with an outlook narrowed by specialised training. Each wants by intensive study to find fundamental characters upon which to base further subdivision. But it is sometimes good to get out of the groove of specialism and to look about a bit to obtain a more comprehensive view.

The aeroplane helps to restore the perspective: it gives the Brobdingnagian view. For the Lilliputian, general advice is given in procedure, how to look at aerial photographs and interpret what he sees. Viewed from the air the land surface of a physiographic region (e.g. the London Basin) discovers itself in "regions"—natural units of country—which are recognised in much the same way as one recognises a plant community. It is often, however, marked by topographical features and is named after a physiographic feature or usually the geological formation. For example, in the London Basin there are six "regions" of which "E. P. Reading outcrop" is one, where E. P. indicates that the outcrop of Reading beds falls within a grouping of "regions" with "low escarpment and undulating plateau." The "region" is made up of smaller units called "sites," defined as areas which appear, for all practical purposes, to provide throughout their extent similar local conditions as to

climate, physiography, geology, soil and edaphic factors in general. In the Reading Outcrop Region there are twelve sites: Reading Sand over Clay is one, written in shorthand RS/RC.

A general description of each region is given, including some account of the topography, the farming, both arable and grassland, forests and their management, the natural or semi-natural vegetation, together with notes on the presence or absence of hedges, the species of hedgerow trees and their growth, and a number of other features, e.g. the lay-out of farms and roads. The sites of each region are noted: in some regions they are treated in consider-able detail and mapped.

In old and surveyed countries much of the requisite information regarding the grosser features could be obtained from good maps, and anyone with an eye for country, as Bourne has, could supplement this in the field. But aerial photographs aid in the finer delimitation of sites and shorten the time required in a survey. In new countries the use of the aeroplane is strongly recommended: regions and sites are easily recognised and mapped, sites are sampled on the ground and estimates made of the stock and the potentialities of the habitat.

It has long been recognised by the rural population that the countryside is divisible into "countries," often quite small units, and what the countryman says is worth con-sideration and respect. But differences between "countries" imply a good deal more than geological and soil differences—although these are important—and are primarily, although by no means exclusively, based on some difference in the microclimates. It seems a pity that in this definition of a "region" a comprehensive basis was not adhered to, so that farmer, forester, geographer, etc., could accompany each other farther along the common road. For example, an attempt is made to assign some of the beech woods of the Chiltern plateau to the series described from the South Downs plateau. Now these two areas differ in climate (which Bourne realises) and in soils (which he doesn't) and accordingly from the point of view of finer subdivision—which is one of the aims of ecological research directed to the aid of silviculture—the two should be kept distinct. They belong to different "regions" or "countries." This applies also to the escarpment beech woods, where the soils are com-parable but the climates distinct, although the two escarpments may be grouped in a unit of a larger or different order, transcending or cutting across "regions" or "countries."

It is a curious fact that foresters have always stressed the importance of geology much more than agriculturists, and the recent trend of soil science confirms the forester's view in a country like ours where the soils are foetal. In a country like Russia it would be a mistake to do so. In the strip surveyed there are rendzina soils, podsols, and brown earths. The first two are easily recognised and subdivided, but the heterogeneous brown earths present a problem in classification which the soil scientist has not yet solved. And it is doubtful if Bourne's method of stressing geological origin will appeal to them. It will also offer great difficulties in those parts of the country overlaid by a thick blanket of drift.

In his search for some stable base on which to set his site units Bourne emphasises the usefulness of vegetation but adds that vegetation must be used with discrimination. This is true and will remain true so long as our knowledge of vegetation remains elementary and so long as an accurate conception of what vegetation is and of its interpretation are not common knowledge or are left to experts. It ought to be clearly understood that where we are dealing with finer distinctions vegetation is not equivalent to the dominant species, and that different plant communities may, from the point of view of the growth of an artificial crop, indicate the same thing. Different stages of the succession, different treatments (e.g. grazing by different animals) imply different facies which are not easily interpreted *per se* but only in relation to a stable background, viz. the climax vegetation. The example given on p. 53 and pp. 117–118 to show the need for care is really a remarkably good instance of the value of vegetation study and correct interpretation. Again, the fact that the ground vegetation under different species of trees on the same site is different, cannot be used as

an argument against the use of vegetation. It merely means that vegetation tells us more and not less than our preconceived hypothesis will accommodate. So too, what I have said in the previous review about tree roots applies here also.

There is much good matter in this memoir, to which reference cannot be made here, but the plea for a land classification and stocktaking is heartily endorsed. The aerial photographs are very eloquent; but at this date one need hardly stress aerial photography as a powerful weapon in the service of the ecologist or regional surveyor.

<div align="right">A. S. W.</div>

Romell, L. G. and **Heiberg, S. O.** Types of humus layer in the forests of the north-eastern United States. *Ecology*, **12**, pp. 567–608, 1931.

The paper represents a first systematic effort to apply outside Europe the principles and method laid down by P. E. Müller in his classical studies on natural types of humus layer. It is also a contribution to the question of classification and nomenclature of forest humus layers in general. After a critical review of the different proposals of classification, the authors conclude that Müller's system fits the natural conditions best. That this holds true for American conditions as well is indicated especially by the flora characteristic of different types of humus layer. A fundamental point of Müller's system is that the classification applies to the entire humus layer (i.e. the top layer of the soil, owing its characteristic features largely to its humus content; no matter whether this content is high or low and whether the humus is "incorporated" or not). The authors strongly oppose the tendency inaugurated by Ramann to classify the humus alone, which is only one constituent of the biological unit. Müller's two main types or groups are retained. They are characterised morphologically, as the Scandinavian school has always done, contrary to the tendencies in Germany, and some types with unincorporated humus are included in the mull group. Specific types listed are crumb mull, grain mull, twin mull, detritus mull, root duff, leaf duff, greasy duff, and fibrous duff. This list is not supposed to cover any variation possible, but is just an enumeration of conditions found to occur within the region studied sufficiently regularly, and characteristically enough developed, to warrant their being recognised as types. The crumb mull is the classical prototype of the mull group, inhabited by large earthworms. The types greasy and fibrous duff have been taken over from the Danish forester Juncker.

The distribution of the types within the region is discussed. Groundwater conditions seem to be a particularly important factor locally. Some plants are listed as indicators of mull and of duff. The most valuable hardwood species of the region seem to be among the mull preferring plants.

Data are presented on nitrification, pH and lime content of the different types. Contrary to European experience, nitrification was found in the laboratory within all types, even pronounced duffs, and down to a pH of 2·9 which was close to the lowest pH value encountered in any sample, whether nitrifying or not. Still, a great difference was found between the types, the mull samples being practically all nitrifying, whereas the majority of samples of pronounced duffs did not nitrify. Storage tests yielded surprisingly high values for root duff and other intermediate forms as compared to the crumb mull, while inoculation tests gave results agreeing better with the expectations from previous experience and with the indications furnished by the vegetation. The puzzling results of the storage tests are ascribed to a "sampling effect" to be discussed in a later paper.

The main data are given in concentrated table form on eight pages. A mimeographed Appendix of 29 pages, distributed by the authors, gives descriptions of 17 chosen localities including vegetation and soil notes, Bouyoucos analyses, etc.

<div align="right">L. G. ROMELL.</div>

BRITISH ECOLOGICAL SOCIETY

SUMMER MEETING AT LOWESTOFT,
MAY 22ND–24TH, 1931

By invitation of the Director, Dr E. S. Russell, O.B.E., a meeting of the Society was held at the Laboratory of the Ministry of Agriculture and Fisheries from Friday May 22nd to Sunday May 24th, 1931.

Members were met on arrival by the Director and Dr Carruthers and conducted to the Laboratory on the Esplanade, where a meeting for communications was held with the President, Prof. Fritsch, in the Chair.

Dr Russell opened the proceedings by welcoming the Society, and then gave a brief account of Marine Fishery research in which he emphasised the essentially ecological character of the problems dealt with. The organisation necessary to cope with the large area investigated was explained—an organisation which utilised the fishing vessels themselves as a valuable source of information for statistical data. The varied character of the investigations was explained, and though these are primarily of economic importance their value in relation to the fundamental ecological problems of animal communities was at once evident. One cannot but regret that the published results, which treat both of the environmental factors and of the autecology of marine organisms, are not more widely known and more easily available to the students of pure science. Dr Russell's paper, which appears in the present issue of the JOURNAL (pp. 128–51), should prove valuable in aiding students to get in touch with the work which has so far been accomplished.

Mr F. M. Davis then gave a short review of the work carried out in 1921–4 on the Ministry's Research vessel *George Bligh* by means of the Petersen Grab, an instrument designed for the quantitative capture of benthic fauna.

Work was carried out in various areas of the North Sea, more especially in the Dogger Bank area. It was shown that in certain years enormous beds of certain animals were found, e.g. the molluscs *Spisula subtruncata* da Costa and *Mactra stultorum* Linn., but that the occurrences of these animals was by no means constant. The question of communities and the preferences of different species for different environments were discussed, and the view was expressed that this "soil fastidiousness" was an important factor influencing the fluctuations of the benthic infauna. It was suggested that, as a general principle, animals with a sedentary adult stage alternating with a passive planktonic stage could only produce new stocks if the currents carrying the planktonic larvae were of such a strength and moving in such a direction that the larvae would be carried into a position where they would find conditions favourable for their further development when the time arrived for the metamorphosis to the bottom stage. This meant that the amplitude of the fluctuations in the stocks of animals of this type would probably be in direct relation to the soil-fastidiousness of the animals. The importance of the fluctuations of the benthic infauna in relation to the concentrations of fish was stressed. It was stated that further extensive work on the distribution of various species and their relative frequency in different environments would be carried out, with a view to estimating the potentialities of various grounds for the production of food for fish. The results have been published in detail in *M.A.F. Fishery Investigations*, Series II, **6**, No. 2, 1923, and **8**, No. 4, 1925.

An account of *Phaeocystis poucheti* in relation to Herring Shoals was then given by Mr R. E. Savage. This is a colonial flagellate which occurs in large concentrations in the

southern North Sea in spring and autumn and produces a condition of the water known to herring fishermen as "baccy juice" which they associate with poor catches. The author's investigations showed that herring do appear to avoid such water, but that the effect of *Phaeocystis* on the migrations of the herring is not always harmful to the fisheries. It diverts herring from their migratory cycle, and in spring, when the herring are moving north after spawning, the normal effect is to cause some of them to approach East Anglian waters and give rise to a fishery there. Under abnormal conditions (e.g. when the wind blows from the East for a prolonged period) *Phaeocystis* drifts westwards, prevents herring from congregating for the Lowestoft spring fishery, and poor catches result. In 1927 the concentration of herring in East Anglian waters for the great autumn fishery was interrupted by a great belt of *Phaeocystis* 100 miles long which caused the herring to swim round it and concentrate some 50 or 60 miles eastward of their usual shoaling ground. Diatoms also produce a "baccy juice" condition of the water, and two species which have their maximum in November—*Biddulphia sinensis* and *Rhizosolenia styliformis*—were considered, but there was no clear evidence that they acted as barriers to herring migrations.

The next communication was by Mr J. R. Lumby, who dealt with the Current Systems of the North Atlantic and the North Sea, a subject of considerable interest not only to the animal ecologist but also to the student of plant dispersal. The usual generalised representation of the surface circulation in the North Atlantic is based mainly on navigational information derived from ships. In using this information for studying the currents certain difficulties are met with, and these are concerned with the reliability of the data and with their interpretation. In recent years greater knowledge of the internal structure of the oceanic water masses has been acquired, and this, in conjunction with a fresh study of the navigational data undertaken by the German oceanographers, has led to some revision of the ideas embodied in the older diagrams. In place of the great whirl in the lower latitudes, the flow is thought to be mainly east and west, the Gulf Stream being regarded as due to the interruption of the zonal currents tending to encircle the earth. The Canaries Current is ill-defined. The motionless central region is replaced by a convergence. Owing to the presence of a sharp discontinuity in the vertical direction, two distinct parts of the sea are recognised, the comparatively shallow upper layer ("troposphere") and the deep under layer ("stratosphere"). The circulation in each layer is complete in itself and the exchange of water in the vertical direction between the two parts is very small. The under layers appear, however, at the surface in polar regions, the lines of separation from the upper layers on the sea surface being termed the polar fronts. Polewards of this line the sinking of water gives rise to the movement of the under layers, the circulation in this case being strongly developed meridionally. Three main currents are distinguished, two equatorwards and an intermediate return current. In the absence of land masses, this circulation would be developed symmetrically about the equator. But, owing to the conformation of the Atlantic Ocean, the southern circulation predominates and extends to about 25° N. lat. The study of the current system in the North Sea differs from that in the Atlantic in that in the former case special investigations furnish our chief source of information. Beginning with the comparatively simple conception, due to Fulton, of a flow round the North Sea in an anticlockwise direction, a more complicated system is now recognised. Water enters from the north with a direction rather east of south. Where this flow runs against the N.E.-going flow from Dover Straits and the stream emerging from the Skagerrack, whirls are set up, which seem fairly constant in position.

The various papers were followed by a number of questions and by discussion, and the President expressed the appreciation of the Society to Dr Russell and the Staff of the Laboratory for the very interesting series of communications. The vote of thanks was seconded by Prof. Salisbury who laid stress on the ample justification which the papers

afforded for the claim of the Director that the work carried on at the Station was fundamentally ecological in character.

The following morning members visited the Fish-market under the able guidance of Mr G. T. Atkinson the District Inspector of Fisheries. Subsequently members were shown the work in progress at the Fisheries Laboratory, and in the afternoon one of the research vessels was visited and inspected.

On the Sunday an excursion was made to the dunes and freshwater marshes at Kessingland under the guidance of Mr Hickling. Prof. Salisbury drew attention to the similarity of the flora on the older dunes to that of the Breckland heaths, among the species noted being *Alchemilla arvensis, Teesdalia nudicaulis* (f.), *Moenchia erecta, Myosotis collina, M. versicolor, Aira praecox, Weingartneria canescens, Lycopsis arvensis, Vicia lathyroides, Trifolium striatum, Trifolium suffocatum* (r.), *Stellaria boreana, Sedum acre, S. anglicum* and *Silene conica* (l.f.). The last named is apparently a new record for the vice-county. This community which is characterised by the abundance of winter annuals may be termed the *Alchemilla arvensis* associes from its most constant constituent. The *Alchemilla arvensis,* here and in similar habitats which are arid in summer, is an erect form, which for convenience may be provisionally termed *forma erecta* as distinct from the *forma prostrata* of arable land. Breeding experiments may however prove these to be hereditary features. The marshes and ditches yielded an interesting flora in which the most noteworthy feature was the frequency of a small-flowered type of *Caltha* with markedly recurved fruits. The marsh flora was somewhat of the fen type, with *Orchis incarnata, Carex disticha* and *Primula veris,* but owing to the late season the vegetation was not sufficiently advanced to judge fully of its composition.

E. J. S.

MEETING AT OXFORD, JANUARY 1ST–3RD, 1932

SOIRÉE IN THE DEPARTMENT OF ZOOLOGY

The members of the Society and visitors were entertained at a Soirée in the Department of Zoology and Comparative Anatomy on the evening of Friday, January 1st, when approximately fifty members and visitors were present.

A number of exhibits dealing with animal ecology had been arranged in the laboratory. Mr Charles Elton showed maps of ant territory and foraging paths of wood ants in the New Forest, Hampshire, and graphs and diagrams demonstrating the ten-year cycle in rabbit and lynx numbers in Northern Canada: also the insect faunas (collections) of Greenland, Spitzbergen and Akpatok Island, with photographs obtained by the various expeditions sent out by the Oxford Exploration Club. Mr A. D. Middleton exhibited specimens of grey and of black squirrels, with a map of the distribution of the American grey squirrel in the British Isles. Mr D. H. Davis demonstrated an apparatus for recording diurnal and nocturnal activity of mice and their periods of feeding. Mr J. Ford showed the effects of mole and mice burrows upon the insect fauna of the soil. Mr R. M. Ranson exhibited specimens of field voles (*Microtus*) and lemmings (*Lemmus*) bred in captivity.

During the evening visitors and members were entertained to refreshments, and the most cordial thanks of the Society are due to the Head and Staff of the Department for a very pleasant and successful evening.

ANNUAL MEETING

The eighteenth Annual Meeting of the Society was held in the Botanical lecture theatre on the following morning, Saturday, January 2nd at 10 a.m., the President, Prof. F. E. Fritsch, occupying the chair. The minutes of the previous Annual Meeting were read and confirmed.

In the absence of the Hon. Treasurer, Prof. Tansley presented the accounts and balance sheet of the Society. Comparing the income and expenditure with those of the previous year, he pointed out that there was no marked change in the amounts of the various items except for the outstanding facts that about £150 more had been spent on the JOURNAL, while the receipts from the sale of back volumes were down by £200, the sales of complete sets having entirely ceased. The result was that in place of the profit of about £250 for 1930 there was a deficit of about £100 for 1931. Thanks to accumulated reserves the deficit could be easily met, but the large number of pages published in 1931 (492 besides Supplements) could not be maintained and the Council had decided to go back to the number of pages published in 1930, i.e. about 400. The necessity was regrettable because the pressure to publish the increasing supplies of excellent contributions was greater than ever. The accounts were passed subject to audit (p. 231).

Prof. Tansley reported that the Council had decided that it would be desirable to have the accounts of the Society audited professionally, and the meeting confirmed the decision of the Council. It was proposed by the President and carried unanimously that the very hearty thanks of the Society should be offered to Mr Paulson for his long and valuable services as Hon. Auditor to the Society.

Mr Elton gave an account of the probable scope and size of the proposed new *Journal of Animal Ecology*, and after a short discussion it was proposed by Dr H. Hamshaw Thomas that the decision of the Council to proceed immediately with the preparation of the new journal be confirmed. This was seconded by Dr Woodhead and carried unanimously.

The Hon. Secretary then presented his report of the work of the Society during the past year and this was adopted.

Hon. Secretary's Report for the Year 1931

The seventeenth Annual Meeting of the Society was held in the Botanical Department of East London College on January 10th, 1931. On the previous evening members and guests were entertained at a Soirée at East London College at which numerous exhibits were shown. The thanks of the Society are due to Prof. and Mrs Fritsch, the Staff of the Botanical Department and to the Governors of East London College for the hospitality provided.

A Meeting was held from Friday, May 22nd to Sunday, May 24th at the Research Laboratories of the Ministry of Agriculture and Fisheries at Lowestoft, at which a number of papers were communicated and exhibits of the work carried on were shown. It is much to be regretted that more members were not able to avail themselves of this opportunity. Those members who attended are much indebted to the Director, Dr E. S. Russell, and his Staff for a most interesting and instructive meeting and for the admirable arrangements made for their entertainment.

An excursion, which was very well attended, was held on Saturday, October 17th at High Wycombe, in conjunction with the British Mycological Society, under the guidance of Mr Ramsbottom and the Hon. Secretary.

During the past year two numbers of the JOURNAL have been issued, in February and August respectively, together comprising 492 pages, supplements of 39 pages, and 28 plates·

The Society's Transplant Experiments at Potterne continue satisfactorily, and Mr

Marsden-Jones and Dr Turrill hope to prepare a second report upon them in the near future.

We deeply regret to record the loss by death of Dr T. F. Chipp, who was a constant attendant at our meetings and excursions and whose cheerful presence we shall greatly miss.

Twenty-six members have resigned or their names have been removed from the membership list owing to the lapse of their subscriptions. Fifteen new members have joined the Society, the membership of which now totals 242.

This number is actually twelve less than at this time last year, but it should be mentioned in this connection that in the last report there were included several whose names had been retained in the list although they were already not in receipt of the JOURNAL owing to their subscriptions being in arrear.   E. J. SALISBURY, *Hon. Sec.*

Dr Turrill made a brief statement, illustrated by lantern slides, on the transplantation experiments of the Society at Potterne on non-calcareous and calcareous sand, and on non-calcareous and calcareous clay. He reported the discontinuance of the experiments on *Silene vulgaris* and the reduction to one half of the area allocated to *Anthyllis vulneraria*. In the space so liberated pure lines of *Phleum pratense*, provided by Dr Gregor, and *Fragaria vesca* were to be grown. Dr Turrill indicated that a second report was in preparation for publication in the JOURNAL, and in reply to Prof. Matthews stated that regular soil analyses were being made in all the beds and the processes of soil formation were being followed by Mr C. G. T. Morison of Oxford, who was also analysing the plant substance formed on different soils by *Centaurea*. Prof. Tansley expressed the appreciation of the Society for the energy and enthusiasm of Dr Turrill and Mr Marsden-Jones in their prosecution of the transplant work.

Prof. Salisbury having indicated that pressure of work compelled him to relinquish the office of Secretary, the President proposed a very hearty vote of thanks for his extremely valuable services as Hon. Secretary to the Society for the past fifteen years: this was seconded by Prof. Boycott and was carried unanimously and with acclamation. Prof. Tansley also spoke of the great indebtedness of the Society to the retiring Secretary.

The meeting proceeded to the election of officers as follows:

President: Prof. A. E. BOYCOTT, F.R.S.

Vice-President: Mr C. S. ELTON.

Hon. Editor: Prof. A. G. TANSLEY, F.R.S.

Hon. Secretary: Dr H. GODWIN.

Council Members: Mr E. PRICE-EVANS, Prof. E. J. SALISBURY, Dr M. MACGREGOR SKENE, Dr A. S. WATT.

The newly elected President having taken the chair, Prof. Tansley gave an account of the first-year course in Botany and especially in Elementary Ecology given by him to Forestry students at Oxford. He indicated how students were introduced at once in the field to definite examples of well known plant communities such as oak and beech woods, and how this field work commenced at the outset was correlated with the lectures and with the progress of the general botanical courses which they attended. He explained that the course had three main objects: (*a*) to instil the habit of examining and becoming familiar with individual plant species, (*b*) to instil the habit of examining types of vegetation in the field, and (*c*) to supply sufficient theory for the organisation of these observations. Prof. Tansley emphasised the importance of Ecology as a basis of Forestry pursued in tropical climates where natural or semi-natural forests are the rule. Prof. Troup, Head of the Oxford School

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR 1931

Income

	£ s. d.	£ s. d.
Subscriptions received including arrears less prepayments for 1932 carried to Balance Sheet below ...	292 4 6	
less prepayment	11 5 0	280 19 6
Interest on Investments ...		42 10 0
Interest on Deposit Account ...		5 4 0
Journal of Ecology—Sales, etc.:		
Current volume xix, 1931 ...	455 17 0	
Back volumes and parts ...	46 2 10	
Advertisements ...	6 2 1	
Sale of reprints—Aircraft Operating Co., Ltd. ...	10 0 0	518 1 11
		846 15 5
Journal of Animal Ecology (proposed)—Grant from the Royal Society in aid of Guarantee Fund carried to Balance Sheet below ...	100 0 0	
Debit balance—Deficit for year ...		99 0 3
		£945 15 8

Expenditure

	£ s. d.	£ s. d.	£ s. d.
Working Expenses:			
Printing Circulars, etc. ...	7 1 0		
Postages, etc. ...	6 6 2		
Bank Charges ...	0 1 3		
Clerical Assistance (Secretary and Treasurer) ...	15 0 0		28 8 5
Fresh Water Biological Association of the British Empire—Grant in aid ...			10 0 0
Soirée Expenses ...			4 2 6
Journal of Ecology:			
Paper, Printing, Illustration, etc. ...	784 9 4		
Binding ...	3 11 3		
Postage, etc. ...	40 13 6		
Insurance of Stock ...	2 2 3		
Publishers' Commission ...	76 16 2		
Back parts purchased ...	20 0 0	927 12 6	
less Prepayment of Blocks for 1932 Journal ...		24 7 9	903 4 9
			£945 15 8

BALANCE SHEET AT 31ST DECEMBER, 1931

Liabilities

	£ s. d.	£ s. d.
Subscriptions prepaid for 1932 ...		11 5 0
Journal of Animal Ecology (proposed) Guarantee Fund received and carried forward ...		100 0 0
General Revenue Account—Balance of Funds:		
Surplus at 31st December, 1930 ...	989 3 1	
less Deficit from Revenue Account 1931, above ...	99 0 3	890 2 10
		£1001 7 10

Assets

	£ s. d.	£ s. d.
Westminster Bank—Credit Balances:		
Current Account ...	21 7 1	
Deposit Account ...	40 0 0	61 7 1
Journal, 1932—Prepayment of blocks ...		24 7 9
Investments:		
£700 5 % War Loan 1929/47 at cost... (Market value at 31st December, 1931, at 95½, £668. 10s. 0d.)	717 3 0	
£200 5 % Conversion Loan 1944/64 at cost (Market value at 31st December, 1931, at 99, £198. 0s. 0d.)	198 10 0	915 13 0
		£1001 7 10

NOTE.—A further asset is the unsold stock of the *Journal* held for the Society by the Publishers.

Audited and found correct and as shown by the Account Books of the Society. The items Bank Balance and Investments have been verified by Bank Certificates.

(signed) WM. NORMAN & SONS,
Chartered Accountants.

26th January, 1932

H. BOYD WATT,
Hon. Treasurer.

of Forestry and Director of the Imperial Forestry Institute, also spoke of the value of ecological training to forestry students.

Mr Elton showed a map of the nests and trackways of wood ants (*Formica rufa*) in Dr Longstaff's bird sanctuary in Hampshire. The territories of the different nests are determined mainly by the occurrence of birch trees which support aphids that are tended by the ants, and there is no communication between the different nests except during occasional conflicts. The territories are of very similar area and are often divided from one another by straight lines.

The Meeting adjourned at 12.45 and resumed at 2.15 p.m.

Mr H. Baker described the results of acidity determinations of the principal rocks found in the vicinity of Oxford and of the soils formed from them. The Oxford and Kimmeridge clays, the Calcareous Grit and Coral Rag were all strongly alkaline but tended to become more acidic on weathering, the calcareous grit giving by continued leaching extremely acid woodland and heath soil. Soils derived from these rocks and from Greensand were compared in woodland, grassland and marshy sites. The grassland soils on the clays were still either alkaline or only slightly acid. Prof. Salisbury drew attention to the inverted acidity gradients shown in some of Mr Baker's results, and causes were suggested.

Mr W. H. Wilkins gave an account of the distribution of the higher fungi in ten areas situated on chalk, clay and greensand, and bearing oak wood, beech wood and heath. A comparison of the number of species common to different groupings of the various areas suggested that the mycological content was determined more by the nature of the sub-soil than by the dominant vegetation. The woodland fungi could be classed as: parasites, saprophytes, mycorrhizal fungi, associated fungi and independent fungi, and various examples of the association of fungi with specific forest trees were discussed.

Capt. C. Diver spoke of the work carried out by himself and his son on the distribution and ecology of grasshoppers on Studland Heath, Dorset. Nine species were found and some of the factors limiting the distribution of these species were determined. It was shown by the examination of a series of maps of different dates that striking physiographic changes had taken place in the area during recent years and that by a knowledge of these the first appearance of many of the natural features could be dated with reasonable accuracy.

During the course of the afternoon the President read a telegram from the Hon. Treasurer conveying apologies for absence and good wishes for the Meeting.

The Meeting then adjourned for tea, which was kindly provided by the Botanical Department.

The Meeting was resumed at 10 a.m. on the following day in the Department of Zoology and Comparative Anatomy.

Dr A. R. Clapham outlined the statistical principles underlying estimates of vegetation by sampling methods, such as those involving use of the metre quadrat, and showed that it would be expected that long narrow strips of $4 \times \frac{1}{4}$ m. would give less variance for a given area examined. He described an investigation of grassland (fixed sand dune) vegetation in Aberdeenshire supporting his statements and concluded by recommending the strip as the more economical method of sampling, and superior also in other ways to the quadrat.

Mr W. B. Alexander gave an account of the Oxford bird census originated by Mr E. M. Nicholson and carried on by the Oxford Ornithological Society. He described three main lines of work: (*a*) ringing individual birds and examination by a trapping system, (*b*) study of individual species by counting, and (*c*) an extended study of all the bird species on a given area. The results of ringing herons showed scattering of birds in all directions over the country; the Oxford census of rooks dealt with in the JOURNAL for 1930 had been much extended and a martin survey had also been begun. The five years' survey of an area of 125 acres on the old University Farm at Sandford-on-Thames showed an increase in numbers

attributable mainly to five species of birds which form flocks and feed on the fields: the hedgerow bird population remained roughly constant.

Mr T. H. Harrisson described faunal changes brought about in the Island of St Kilda between the time of its evacuation and his visit in the summer of 1931. Remarkable decreases had already occurred in the numbers of starlings, hooded crows and tree-sparrows: he anticipated that substantial increases would take place in the numbers of other species such as Leach's fork-tailed petrel, gannet and puffin. The present bird population was estimated to include 288 pairs of land birds and 9 pairs of predaceous birds, which however did not prey on the land birds. Rock pippits constituted about 60 per cent. of the land birds and were often found away from the coast. In the discussion which followed Dr G. V. H. Carpenter compared the biological results of isolation in St Kilda with those he had seen himself in an island in Lake Victoria.

Mr A. D. Middleton outlined his experiences in organising an ecological intelligence service, compared the merits and demerits of different types of observer, and indicated the best methods of making contact with new observers. He suggested the compilation of a panel of reliable observers available for survey purposes.

Dr Woodhead proposed a vote of thanks to the Heads of the Departments of Botany and of Zoology and Comparative Anatomy for the hospitality extended to the Society at the Meeting and at the Soirée on the preceding evening, and to Mr Elton and Dr Clapham for the trouble taken in organising the meeting. This vote was heartily accorded, and the meeting adjourned at 1 p.m.

An excursion was made in the afternoon under the leadership of Mr Alexander to the vicinity of Fyfield, where flocks of starlings, estimated to amount to perhaps half a million birds, were seen coming to roost in a larch plantation on land belonging to St John's College. An excellent view of the flight to the roost was obtained from the top of an adjacent haystack. The starlings began to come in about 3.40, at first in small groups. The size of the flights rapidly increased to several thousand each, the single flights often exceeding 100 yards in length. On approaching the plantation the whole flight would often rise and wheel once or twice, the birds always alighting in the trees against the wind. Some of the flights landed in adjacent grass fields, blackening the ground, and remaining motionless for many minutes before flying to the wood. The roosting flights were apparently ended by about 4.20, just before it became really dusk. The wood, which was briefly inspected before the starlings arrived, had a strong, rather ammoniacal smell. The ground vegetation seemed to be mainly elder and nettle.

LIST OF MEMBERS (January, 1932).

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, Dr H. Godwin, Botany School, Cambridge.

Adams, C. C.; New York State Museum, Albany, New York, U.S.A.
Adamson, Prof. R. S., M.A.; The University, Cape Town, S. Africa.
Allan, Dr H. H.; Plant Research Institute, Palmerston North, N.Z.
Allee, W. C.; Zoology Building, University of Chicago, Chicago, Ill., U.S.A.
Allen, Miss D. M., B.Sc.; 52, College Street, Chilvers Coton, Nuneaton.
Allorge, Pierre; Laboratoire de Cryptogamie, 63, Rue de Buffon, Paris.
Alun-Roberts, R.; Agricultural Dept., University College, Bangor.
Andersonian Naturalists' Society (cf. Glasgow).
Andreànszky, Baron Gábor; Budapest, VIII, Múzeûm-Körur 4, Hungary.
Armitage, Miss E.; Dadnor, Ross, Herefordshire.
Ashby, Eric, B.Sc.; 18, Shortlands Road, Shortlands, Kent.
Aston, B. C.; P.O. Box 40, Wellington, N.Z.
Bacon, Mrs Alice; The Technical College, Brighton.
Ballard, F., B.Sc.; The Herbarium, Royal Botanic Gardens, Kew.
Barber, Miss E. G.; Harborne, Westbourne Avenue, Emsworth, Hants.
Barnes, Dr B.; 28, Torridon Road, London, S.E. 6.
Barrington, A. H. M.; c/o Messrs Cook and Son, Ltd., Berkeley Street, Piccadilly, W. 1.
Bates, G. H., B.Sc.; Hill House, King's Lynn, Norfolk.
Bell, Prof. H. P.; Dalhousie University, Halifax, Nova Scotia.
Bews, Prof. J. W.; University College, Pietermaritzburg, Natal.
Bharucha, F. R.; Collège des Écossais, Plan des Quatre Seigneurs, Montpelier, France.
Bird, Prof. R. D., M.Sc., Ph.D.; University of Oklahoma, Norman, Oklahoma, U.S.A.
Bishop, Miss M. K.; The Botanical Dept., The University, Manchester.
Blackman, Prof. V. H., F.R.S.; Imperial College of Science, London, S.W. 7.
Blatter, Father E.; St Xavier's College, Bombay.
Bloomer, H. H.; Longdown, Sunnydale Road, Swanage, Dorset.
Bor, N. L., M.A., B.Sc.; c/o Forest Officer, Gauhati, Assam.
Børgesen, Dr F. C. E.; Botanisk Museum, Gothersgade 130, Copenhagen.
Borthwick, Dr A. W.; 25, Drumsheugh Gardens, Edinburgh.
Boycott, Prof. A. E., F.R.S.; 17, Loom Lane, Radlett, Herts., *President.*
Boyd, A. W., M.C., M.A.; Frandley House, nr Northwich, Cheshire.
Bracher, Miss Rose, Ph.D.; Dept. of Botany, The University, Bristol.
Braid, Major K. W.; 6, Blythswood Square, Glasgow.
Braun, Miss E. L.; 2702, May Street, Cincinnati, Ohio, U.S.A.
Brenchley, Dr Winifred E.; Rothamsted Experimental Station, Harpenden, Herts.
Brodsky, Prof. A.; Middle Asiatic State University, Tashkent, Usbekistan, U.S.S.R.
Brooks, F. T., M.A.; Botany School, Cambridge.
Burnett, Miss I. M.; Malvern Girls' College, Worcestershire.
Burtt, B. D.; Botanist, Tsetse Research, Kondoa Irangi, Tanganyika Territory, E. Africa.
Butcher, R. W., B.Sc.; The Tees Laboratory, Barnard Castle.
de Caen, Mrs, Ph.D.; Springfield, Delgany, Co. Wicklow, Ireland.
Calvert, J., M.Sc.; 47–49, Brookland Street, Belfast, N. Ireland.
Carter, Dr Nellie; E. London College, Mile End Road, London, E. 1.
Cavers, Dr F.; *Hon. Life Member.*

Chambers, Miss W. E., B.Sc.; Innesbrook, Watlington, Oxon.
Christophersen, Prof. E.; B.P. Bishop Museum, Honolulu, T.H.
Clapham, Dr A. R.; Botanical Dept., The University, Oxford.
Clements, Prof. F. E.; Mission Canyon, Santa Barbara, California.
Cockayne, Dr L., F.R.S.; Ngaio, Wellington, New Zealand.
Colville, Miss E. G.; Arngomery, Kippen, Stirlingshire, Scotland.
Cooper, Prof. W. S.; Dept. of Botany, Univ. of Minnesota, Minn., U.S.A.
Cotton, A. D.; The Herbarium, Royal Botanic Gardens, Kew.
Cowles, Prof. H. C.; Univ. of Chicago, Chicago, Ill., U.S.A.
Croydon Natural History and Scientific Society, Public Hall, Croydon.
Curtis, Miss W. M., B.Sc.; 12, Blenheim Road, Caversham, Reading, Berks.
Cutting, E. M., M.A.; 125, Tredegar Road, Bow, London, E.
Czeczott, Mrs Hanna; Botanical Inst., Lubicz 46, Cracow, Poland.
Darbishire, Prof. Otto V.; Botanical Dept., University, Bristol.
Davey, Miss A. J., M.Sc.; Univ. Coll. of N. Wales, Bangor, N. Wales.
Davies, W. C.; The Cawthron Institute, Nelson, N.Z.
Davis, D. H. S.; Amberley Farm, Amberley, Stroud, Glos.
Davy, Dr J. Burtt; Imperial Forestry Institute, Oxford.
Dawson, R. B., M.Sc., F.L.S.; St Ives Research Station, Bingley, Yorkshire.
Deam, C. C.; Bluffton, Indiana, U.S.A.
Delf, Dr E. M.; Westfield College, Hampstead, London, N.W. 3.
Dowling, Miss R. E., B.Sc.; The Nest, Ledgers Road, Slough, Bucks.
Doyle, Prof. J.; Botany Dept., University College, Dublin.
Drabble, Dr Eric; Moons Hill, Freshwater, Isle of Wight.
Du Rietz, Prof. Einar; Vaxtbiologiska Institutionen, Upsala, Sweden.
Eden, T.; Tea Research Institute, St Coombs, Talawakelle, Ceylon.
Ekblaw, Dr W. E.; Clark University, Worcester, Mass., U.S.A.
Elton, C. S.; Dept. of Zoology, Univ. Museum, Oxford.
Essex Field Club, The (Essex Museum of Natural History, Romford Road, Stratford, Essex).
Evans, E. Price; White Broom, 69, Westgate, Hale, Cheshire.
Farmer, Prof. Sir J. B., F.R.S.; St Leonards, Weston Road, Bath.
Featherly, Prof. H. I.; Oklahoma Agricultural and Mechanical College, Stillwater, Okla., U.S.A.
Fenton, E. Wyllie; 13, George Square, Edinburgh.
Fraser, G. K., M.A., B.Sc.; Forestry Dept., Marischal College, Aberdeen.
Fritsch, Prof. F. E.; Danesmount, Tower Hill, Dorking.
Fuller, Prof. G. D.; Botany Dept., The University, Chicago, Ill., U.S.A.
Gams, Dr H.; Innsbruck-Hotting, Bauerngasse 15, Austria.
Gibson, Miss C. M.; The Municipal College, Portsmouth.
Gilbert-Carter, H., M.A., M.B.; Cory Lodge, Botanic Garden, Cambridge.
Gilmour, J. S. L., B.A.; Clare College, Cambridge.
Gleason, Dr H. A.; N.Y. Botanical Gardens, New York City, New York, U.S.A.
Glasgow and Andersonian Nat. Hist. and Microscopic Soc.; Societies Rooms, Royal Technical College, Glasgow.
Godwin, H., Ph.D.; Botany School, Cambridge, *Hon. Secretary.*
Good, Prof. R.; Univ. College, Hull.
Gourlay, W. B., M.A., M.B.; 7, Millington Road, Cambridge.
Green, Miss M. L.; 4, Mortlake Road, Kew, Surrey.
Griffith Tedd, H.; P.O. Box 30, Xanthie, Greece.
Griffiths, B. M., D.Sc.; Dept. of Botany, Univ. Science Labs., South Road, Durham.

Gunawardena, D. C., B.A.; 41, Aberdeen Park, Highbury, London, N. 5.

Halket, Miss A. C., B.Sc.; Bedford College, Regent's Park, London, N.W. 1.

Halliday, W. E. B.; Greenbush, via Prairie River, Sask., Canada.

Hands, Mrs; Beachfield, The Folly, Radlett, Herts.

Hanson, Dr Herbert C.; Botanist and Head of Dept. of Botany, North Dakota Agric. College and Expt. Station, Fargo, North Dakota, U.S.A.

Hare, C. Leighton, B.Sc.; Greenmount, Cleeve Hill, nr Cheltenham.

Harrisson, T. H.; Pembroke College, Cambridge.

Hayes, T. R.; Dept. of Agriculture, The Gambia, B. West Africa.

Heddle, R. G., M.A., B.Sc.; Edinburgh and E. of Scotland College of Agric.. 13, George Square, Edinburgh.

Hilary, Miss D., B.Sc.; 15, Plevna Terrace, Bingley, Yorks.

Hill, Sir A. W., F.R.S.; Royal Botanic Gardens, Kew.

Hill, Prof. T. G.; University College, London, W.C. 1.

Holch, Dr A. E.; Peru State Teachers' College, Peru, Nebraska, U.S.A.

Holsinger, E. C. T.; Government Training College, Colombo, Ceylon.

Holttum, R. E., M.A.; The Botanic Gardens, Singapore.

Horne, F. R., B.A.; Seale-Hayne Agricultural College, Newton Abbot, Devon.

Howarth, W. O.; Botany Dept., The University, Manchester.

Hubbard, C. E.; The Herbarium, Royal Botanic Gardens, Kew.

Hume, Miss E. M. M.; 57, Doughty Street, London, W.C. 1.

Hunter, R. E., B.Sc.; Imp. Coll. Trop. Agriculture, St Augustine, Trinidad.

Hutchinson, R. R.; 11, Fryston Avenue, Croydon.

Hyde, H. A., M.A.; National Museum, Cardiff, S. Wales.

Ingold, C. T., M.Sc.; The University, Reading.

Jacot, A. P.; Dept. of Biology, Shantung Christian Univ., Tsinan, China.

Jennings, A. E.; Carnegie Museum, Pittsburg, Pa., U.S.A.

Joaquim, Miss U. I. A., B.Sc.; Woodhall Girls' School, Woodhall Spa, Lincs.

Johnson, Miss Edith; 37, Cavendish Road, Heaton Mersey, Manchester.

Johnstone, Miss Mary; 9, Victoria Avenue, Cheadle Hulme, Cheshire.

Jones, Miss G. M.; The Cottage, Wraysbury, Wilts.

Juliano, J. B.; c/o Dept. of Plant Physiology, College of Agriculture, Univ. of the Philippines, Los Baños, Laguna, Philippines.

Kashkarov, Prof. D.; Tashkent, Novaia 19, Usbekistan, S.S.S.R. (Russia).

Kawada, Prof.; Forest Experiment Station, Meguro, nr Tokio, Japan.

Kessell, S. L.; Conservator of Forests, Forests Dept., Perth, W. Australia.

Laughton, F. S.; Assistant Forest Officer, Concordia, Knysna, C.P., S. Africa.

Leach, W.; The University, Birmingham.

Lewis, Prof. F. J.; Univ. of Alberta, Edmonton, Alberta, Canada.

Lind, Miss E. M., B.Sc., Ph.D.; The University, Sheffield.

Lowndes, A. G., M.A., F.L.S.; Marlborough College, Wilts.

Lüdi, Dr W.; Brunnmattstrasse 70, Bern, Switzerland.

McBeath, D. K.; Ballochyle House, Sandbank, Argyllshire.

McDougall, Prof. W. B.; Univ. of Southern California, Univ. Park, Los Angeles, California.

McLean, Prof. R. C.; University College, Cardiff.

McLuckie, J., D.Sc.; Dept. of Botany, The University, Sydney, N.S.W.

Mangham, Prof. S., M.A.; University College, Southampton.

Marquand, C. M.; 16, York Avenue, East Sheen, London, S.W. 14.

Marsden–Jones, E. M.; The Potterne Biological Station, nr Devizes, Wilts.

Mason, E. W.; Suffield House, Paradise Road, Richmond, Surrey.

Matthews, Prof. J. R., M.A.; The University, Reading, *Vice-President.*

Middleton, A. D.; 7, Thorncliffe Road, Oxford.

Middleton, A. R.; Biological Labs., Univ. of Louisville, Louisville, Kentucky, U.S.A.

Miller, W. B.; U.S. Veterans' Hospital, Walla Walla, Washington, U.S.A.

Milne-Redhead, E., B.A.; The Herbarium, Royal Botanic Gardens, Kew.

Montford, H. M., B.Sc.; 251, Upper Richmond Road, Putney, London, S.W. 15.

Moore, Barrington; 1520, K. Street, N.W., Washington, D.C., U.S.A.

Morris, George, B.Sc.; Collège des Écossais, Plan des Quatre Seigneurs, Montpelier, France.

Morss, W. L., M.Sc.; North Kirkland, Dalry, Ayrshire.

Mukerji, S. K., D.Sc.; Lucknow Univ., Lucknow, India.

Murray, J. M., B.Sc.; 76, Hillview Terrace, Corstorphine, Midlothian.

Negri, Prof. Giovanni; R. Istituto Botanico, via Lamarmora 4, Firenze, Italy.

Newman, Leslie F., M.A.; St Catharine's College, Cambridge.

Newton, Prof. Lily, M.Sc., Ph.D.; Dept. of Botany, Univ. College of Wales, Aberystwyth, Wales.

Nichols, Prof. G. E.; Botany Dept., Yale Univ., New Haven, Conn., U.S.A.

Ogg, W. G., M.A., Ph.D.; Macaulay Inst. for Soil Research, Craigiebuckler, Aberdeen.

Ogha, Prof. Ichiro; Educational Institute, Darien, Manchuria.

Oldham, Charles; The Bollin, Shrublands Road, Berkhamsted, Herts.

Oliver, Prof. F. W., F.R.S.; Egyptian Univ., Abbassia, Cairo, Egypt.

Oliver, W. R. B.; Dominion Museum, Wellington, New Zealand.

Orde-Powlett, Hon. Nigel; Bolton Hall, Leyburn S.O., Yorks.

Orr, M. Y.; Royal Botanic Gardens, Edinburgh.

Osborn, Prof. T. G. B.; Dept. of Botany, Sydney Univ., Sydney, N.S.W.

Osmaston, A. E.; Principal and Professor of Forestry, Forest College, Dehra Dun, U.P., India.

Paltridge, T. B.; Koonamore Vegetation Reserve, Koonamore, S. Australia.

Pammell, Prof. L. H.; Botany Dept., Iowa State College, Ames, Iowa, U.S.A.

Pardy, A. A., B.Sc.; Fuller Siding, P/B Bulawayo, S. Rhodesia.

Paulson, R.; Glenroy, Cecil Park, Pinner, Middlesex.

Pearsall, W. H., D.Sc.; The Botany Dept., The University, Leeds, *Vice-President*.

Pearson, A. A.; Glenside, Madeira Park, Tunbridge Wells.

Perthshire Soc. of Nat. Science (Secretary, John Ritchie); Perthshire Soc. of Nat. Science Museum, Perth, Scotland.

Phillips, Prof. J. F. V., D.Sc.; Univ. of Witwatersrand, Milner Park, Johannesburg.

Pomeroy, Miss F. A., B.Sc.; 110 Pembury Road, Tonbridge, Kent, *Associate*.

Powell, Miss Doris; Aldersyde, Reigate.

Praeger, Dr R. Lloyd; National Library, Kildare Street, Dublin.

Priestley, Prof. J. H., B.Sc.; The University, Leeds.

Ramsbottom, J., M.A., O.B.E.; Botanical Dept., Natural History Museum, London, S.W. 7.

Rayner, Dr M. C.; University of London Club, 21, Gower Street, W.C. 1.

Rees, F. Kenneth; University College, Singleton Road, Swansea.

Rees, J., B.A., B.Sc.; University College, Cardiff.

Regel, Prof. Constantin; The Botanical Garden, Kaunas (Kovno), Lithuania.

Rice, C. H., B.Sc.; 20, Dyson Road, Leytonstone.

Richards, O. W.; 30, Mackenzie Street, Slough, Bucks.

Richards, P. W.; Evreham Lodge, Iver, Bucks.

Robbins, Prof. C. R., M.C., M.A.; c/o Messrs Lloyds Bank, 6, Pall Mall, London, W. 1.

Rübel, Dr E.; Zürichbergstrasse 30, Zürich, Switzerland.

Russell, Dr E. S., The Dolphins, Gills Hill Lane, Radlett, Herts.

Russell-Wells, Miss B., Ph.D.; Botany Dept., University College, London, W.C. 1.

Sager, J. L., M.A.; University College, Exeter.

Salisbury, Prof. E. J.; Willow Pool, Radlett, Herts.

Sandwith, N. Y., M.A.; 2, Observatory Gardens, London, W. 8.

Saunders, Miss E. R.; 10, Newnham Terrace, Cambridge.

Schröter, Prof. C.; Merkurstrasse 70, Zürich, Switzerland, *Hon. Life Member.*

Selwood, Miss G. F.; 49, Blenheim Road, Moseley, Birmingham.

Sernander, Prof. R.; Vaxtbiologiska Institutionen, Upsala, Sweden.

Shantz, Prof. H. L.; Univ. of Arizona, Tucson, Arizona, U.S.A.

Shelford, Prof. Victor E.; Vivarium Building, Wright and Healey Streets, Champaign, Ill., U.S.A.

Sherrin, W. R.; South London Bot. Inst., 323, Norwood Road. Herne Hill, London, S.W. 24.

Shirk, C. J., Ph.D.; Nebraska Wesleyan Univ., Lincoln, Nebraska, U.S.A.

Skene, Macgregor, D.Sc.; The University, Bristol.

Smith, C. A., B.Sc.; The Herbarium, Royal Botanic Gardens, Kew.

Smith, Miss Frances G.; Smith College, Northampton, Mass., U.S.A.

von Soó, Prof. Rudolf, Debrécen, Hungary.

Sperrin-Johnson, Dr J. C.; c/o Union Bank of Australia, Ltd., 71, Cornhill, London, E.C. 3.

Sprague, T. A., D.Sc.; Royal Botanic Gardens, Kew, Surrey.

Stamp, Dr L. Dudley; London School of Economics, London, W.C. 2.

Stanchinsky, Vladimir; Univ. of Smolensk, Smolensk, U.S.S.R. (Russia).

Stapf, Dr O., F.R.S.; The Herbarium, Royal Botanic Gardens, Kew.

Stapledon, R. G., M.A.; University College, Aberystwyth.

Stevenson, Miss E. H.; The Training College, The Close, Salisbury.

Stiles, Prof. W., M.A., F.R.S.; The University, Birmingham.

Storrow, B., M.Sc.; Dove Marine Lab., Cullercoats, Northumberland.

Summerhayes, V. S., B.Sc.; The Herbarium, Royal Botanic Gardens, Kew.

Swabey, C.; c/o Royal Societies' Club, St James Street, London, S.W.

Tansley, A. G., F.R.S.; Grantchester, Cambridge, *Hon. Editor of the Journal.*

Terrell, Miss E. M., B.Sc.; 254, Kidmore Road, Caversham, Reading.

Thoday, Prof. D., M.A.; University College, Bangor, N. Wales.

Thomas, Dr Ethel Miles; University College, Leicester.

Thomas, H. Hamshaw, M.A., Sc.D.; The Botany School, Cambridge.

Thompson, H. Stuart, A.L.S.; 11, Buckingham Place, Clifton, Bristol.

Thompson, Prof. J. McLean; Botanical Dept., The University, Liverpool.

Topham, P., M.A.; c/o Conservator of Forests, Zomba, Nyasaland.

Trapnell, C. G., B.A.; Trinity College, Oxford.

Troup, Prof. R. S., F.R.S.; The Forestry School, Oxford.

Turner, J. E. C.; Deputy Conservator of Forests, Almora, United Provinces, India.

Turner, J. S., B.A.; Selwyn College, Cambridge.

Turrill, W. B., D.Sc.; Royal Botanic Gardens, Kew.

Tutin, T. G., B.A.; 22, Warkworth Street, Cambridge.

Ulekla, Prof. Vladimir; Institute of Plant Physiology, 63, Kaunicova, Masaryk Univ., Brno, Ceskoslovenska (Czechoslovakia).

Vaughan, R. E., B.Sc., A.R.C.S.; Royal College, Cure Pipe, Mauritius.

de Vesian, Miss D. E.; Ladies' College, Cheltenham.

Viguier, Prof. R.; 51, Rue Saint-Martin, Caen.

Vyvyan, M. C., M.A.; Trevedran, Wateringbury, Kent.

Wadham, Prof. S. M.; School of Agriculture, Melbourne Univ., Victoria, Australia.

Waite, Miss B. E.; Museum Cottage, Haslemere, Surrey.

Waller, Dr A. E.; Dept. of Botany, State University, Columbus, Ohio, U.S.A.

Wangerin, Prof. W.; Danzig Langführ. Kastanienweg 7, Danzig.

Warden, Miss W. M.; The Training College, Lincoln.

Watson, W., D.Sc.; Taunton School, Taunton, Somerset.

Watt, A. S., Ph.D.; School of Forestry, Cambridge.

Watt, Hugh Boyd; 90, Parliament Hill Mansions, Lissenden Gardens, N.W. 5, *Hon. Treasurer.*

Weese, Prof. A. O.; University of Oklahoma, Norman, Okla., U.S.A.

Weiss, Prof. F. E., F.R.S.; University, Manchester.

Williams, S., Ph.D.; Botany Dept., The University, Glasgow.

Wilmott, A. J., M.A.; Botanical Dept., Natural History Museum, London, S.W. 7.

Woodhead, Norman; University College, Bangor.

Woodhead, Dr T. W.; The Willows, 35, Longley Road, Huddersfield.

Wright, N., A.R.C.S., B.Sc.; 5, North Square, Hampstead, London, N.W. 11.

JOURNAL OF ANIMAL ECOLOGY

As a result of the wide response to their first announcement, the Council of the British Ecological Society have definitely decided to launch this new journal in 1932. There will be two numbers each year. The first two numbers will be published in the summer of 1932, subsequent numbers in the spring and autumn of each year.

Mr Charles Elton has been appointed Editor, and Mr A. D. Middleton, Assistant Editor. The journal will be printed and distributed by the Cambridge University Press.

Subscriptions of members. The cost of the new journal to members of the British Ecological Society will be 25*s*. per annum (the cost of taking both this and the *Journal of Ecology* being 45*s*.). Subscriptions are payable in advance and should be sent to the Secretary, **Dr H. Godwin, Botany School, Cambridge,** with whom intending members should communicate.

Subscriptions of non-members. For non-members of the Society the subscription is 30*s*. per annum payable in advance. No reduction is made if both journals are taken. These subscriptions should be sent direct or through an agent to **The Cambridge University Press, Fetter Lane, London, E.C.4.**

Other communications (concerning contributions, suggestions, etc.) should be sent to **The Editor, Journal of Animal Ecology, University Museum, Oxford.**

January, 1932

C. S. E.
A. D. M.

PHYTOPLANKTON IN THE ENGLISH LAKES

II. THE COMPOSITION OF THE PHYTOPLANKTON IN RELATION TO DISSOLVED SUBSTANCES

By W. H. PEARSALL.

(With one Figure in the Text.)

In the following pages an attempt will be made to relate the distribution and periodicity of the more important plankton algae to the variations in the characters of the dissolved substances present in lake waters. The data considered for this purpose were obtained in 1928, by periodic collections of plankton and by water analyses from nine of the larger English lakes[1]. The analytical data have already been considered (1). They comprise determinations of phosphate, nitrate, silica, iron, calcium carbonate as carbonate hardness and pH, together with occasional data as to organic matter. In the present communication it is proposed to consider the detailed phytoplankton analyses and their possible relation to the water analyses. It must be recognised from the first that any conclusions drawn from such correlations must be regarded as tentative. They require to be confirmed either by similar analytical studies in other lake areas or preferably by evidence drawn from cultures of the algae under known and controlled water conditions. (Culture experiments are in progress which seem to justify the outlook adopted in this paper.) The correlations indicated here are regarded primarily as clues in the attempt to determine the nature of the factors influencing algae periodicity and distribution rather than as final conclusions.

METHODS.

The plankton was collected by towing a fine net—60 meshes to each centimetre—near the surface of the water. All of the collections for any one lake were made at the same place and in a uniform manner. Owing to the paucity of plankton in some of the lakes, especially Wastwater, and the distances to be covered in making the collections, it was not possible to use more accurate methods of collection. The collections from all lakes were made on two successive days at intervals of one month in summer and about six weeks in winter. The material was examined immediately after collection and five hundred to one thousand organisms (preferably the latter) counted in each sample. In this way the percentage composition of the phytoplankton was estimated. I am very greatly indebted to my father, W. Harrison Pearsall, for assistance in making these counts and in identifying doubtful species.

This method of recording the results has its obvious limitations. It tells nothing about the numbers of organisms present, but it is the best available in view of the method of collection. It seems, moreover, to be adequate for the purpose of the present enquiry. *The problem is, to relate the variations in the proportions of the major groups of plankton algae to the more definite changes in the dissolved solids in the waters.* Thus, if the percentage of any one group (or species) *A* goes up, it will be legitimate to regard this change as being favoured by any corresponding change in solutes which may have preceded it, although the actual sequence of events may be either that group *A* has increased in numbers or that other groups have declined in number. At the same time, it should be stated that previous experience in these lakes has shown quite definitely that "percentage maxima" are normally also the actual number maxima. The principal differences in this respect are observed at the end of the diatom phase, when for a month or so the percentage of diatoms remains high although the actual numbers decrease enormously. Errors in such cases are easily avoided and do not, it will be seen, affect the general reliability of the conclusions.

<div align="center">ANALYSIS OF DATA.</div>

In considering the relations between dissolved substances and algae periodicity, it is advantageous to begin by contrasting the simplest type of periodicity with the complications which may develop from it. The simplest periodicity is that of the rocky lakes (Wastwater and Ennerdale) in which the phytoplankton consists almost entirely of green algae—chiefly desmids—and increases to a maximum about September. The most general complication of this simple type is the development of a diatom maximum in winter and spring. As this diatom phase occurs in all the lakes under consideration except the two most rocky, it is a convenient starting-point for these enquiries. The salient feature of the seasonal changes in the dissolved substances, particularly phosphate, nitrate and silica, is that these substances are much more abundant during the winter period occupied by the diatom phase, and they fall to much lower concentrations during the summer when green algae are most abundant. It would, therefore, be attractive to suppose, *firstly*, that the diatoms require (or can endure ?) these nutritive substances in much higher concentrations than the green algae. The problem cannot, however, be quite so simple because there are cases known in which diatoms materially increase in proportion during the summer period, and in some lakes, for example, Ullswater, diatoms are relatively abundant and dominant all the year round. It will be pertinent to ask secondly, therefore, what are the possible causes for the disappearance of diatoms in other lakes in summer?

The attempt to obtain some idea of the general conditions under which the diatoms develop has been carried out by collecting the analytical data for all those samples which were followed by a marked increase in the proportions of diatoms, up to the time of the number maximum. Generally speaking, the

analyses at the time of the maximum are not of greatest importance because the diatoms decrease afterwards.

They are included, however, in the following table, which summarises the conditions under which *Asterionella gracillima* and *Tabellaria fenestrata* were found developing in 1928. In drawing up values for the maxima and minima of the various substances, a certain amount of discretion has been used, particularly in regard to silica. Very low values of silica occurring at a period of maximum diatom abundance have been disregarded. Possibly a similar treatment might have been applied to the very high nitrate values for *Tabellaria*, Bassenthwaite 6 and 11, both of which occurred when the diatom had reached its maximum. Of the *Asterionella* figures, the phosphate and nitrate values of Derwentwater, 9, are below the limits given. *Tabellaria* was the chief diatom at this time and there was little *Asterionella* present, but it was abundant in the following collection (11). The average figures of analyses 9 and 11 might thus give a better approximation to the lower limits for phosphate and nitrate.

If reference is first made to the observed maxima and minima of the various dissolved substances for *Tabellaria* and for *Asterionella*, it will be found that *Asterionella* normally occurs when the dissolved substances, particularly nitrate, phosphate and calcium are more abundant. Hence this diatom may be regarded as requiring a higher nutritive level than *Tabellaria*. The conditions of Windermere 3–5, and Esthwaite 1–3, resulted in very large maxima of this organism, particularly in the latter case. In contrast, Bassenthwaite, 5, should be regarded as nearly ideal for *Tabellaria* which was abundant at this time and which developed an exceptional maximum in June. Taking the minimum figures for *Asterionella*, and comparing them with the detailed analyses for *Tabellaria*, it will be found that in every case, except one, the analyses for *Tabellaria* conditions are in some respect at or below the minima for *Asterionella*. The significant figures are printed in heavier type. The only exception is for Bassenthwaite, 3, which seems, from the analysis alone, to represent very suitable conditions for *Asterionella*. This diatom was in fact at, or near, a maximum at this time forming 60 per cent. of the plankton, though it was replaced by *Tabellaria* in the following month. It is not intended to argue that the composition of these dissolved substances is the only factor affecting the competition between these two diatoms, indeed other factors are known, so that the presence of such partial exception hardly affects the general conclusion which has been drawn, that *Asterionella* normally occurs in solutions of a higher nutritive level than those favouring *Tabellaria*. The same method has been applied to the other diatoms present in these lakes, but owing to the paucity of data, little can be said about any of them except *Melosira granulata*. This diatom has approximately the same limits as *Asterionella*, but it also occurs in abundance when the carbonate hardness is as low as 3·0 (Crummock, 1–3). It may thus replace *Tabellaria* in the lakes with water of lower calcium content, when the nutritive conditions for nitrate and

phosphate are more favourable. The noteworthy feature about this *Melosira* is, however, its correlation with the Myxophyceae. It only occurs in any abundance in those lakes, Crummock, Lowes Water, Windermere and Esthwaite, which have a considerable Myxophycean element in their plankton, and, in Esthwaite and Windermere particularly, it occurs *before* the main diatom maximum, developing during December when Myxophyceae are still abundant or dominant. It is suggested, therefore, that the abundance of this organism is conditioned (in contrast to *Tabellaria* and *Asterionella*) by those factors which, in summer, bring about large Myxophycean maxima.

Table I. *Conditions under which abundant* Tabellaria *developed in* 1928.

Lake	Month	Phosphate P	Nitrate N	S_1O_2	$CaCO_3$	Remarks
Crummock	3	0·010	0·060	1·2	**3·0**	Maximum followed
	9	**0·0007**	**0·045**	1·3	**3·0**	Few present
	11	0·0021	**0·055**	1·3	**3·0**	
	12	0·0027	0·090	1·1	**2·5**	Maximum
Derwentwater	1	**0·001**	0·060	1·7	3·0	
	3	0·007	**0·055**	0·9	3·0	Maximum
	7	0·002	**0·005**	0·7	5·5	N.B. The calcium content of Derwent-
	8	**0·0013**	**0·020**	0·5	**2·0**	water is 2·5 units higher than is indicated by the carbonate hardness
	9	**0·0010**	**0·040**	1·0	3·0	Maximum
Bassenthwaite	3	0·005	0·085	1·7	7·0	*Asterionella* maximum
	5	0·0025	0·085	0·7	**5·0**	Probably ideal
	6	**0·001**	0·100	0·1	8·5	A huge maximum
	8	**0·0009**	**0·030**	0·5	10·0	
	9	**0·0007**	0·063	1·4	7·5	
	11	0·0027	0·120	2·2	4·7	
Ullswater	1	**0·002**	0·100	2·1	12·5	
	6	**0·002**	0·080	0·5	12·5	
	7	**0·001**	**0·030**	0·8	10·0	
Range of values:						
Minimum		0·0005	0·005	0·5	3·0	
Maximum		0·010	0·100	2·2	12·5	

Conditions under which abundant Asterionella *developed in* 1928.

Derwentwater	9	0·001	0·040	1·0	3·0	Few present
	11	0·003	0·060	1·2	3·0	See note in preceding table on calcium
	12	0·0027	0·100	0·8	3·5	content
Bassenthwaite	1	0·003	0·150	2·3	12·0	
	3	0·005	0·085	1·7	7·0	Maximum
	11	0·0027	0·120	2·2	7·75	
	12	0·0025	0·160	1·5	8·75	
Ullswater	3	0·010	0·085	2·2	11·0	
	5	0·004	0·075	1·0	8·0	
	6	0·002	0·080	0·5	12·5	Maximum
Windermere	12	0·0027	0·18	1·0	9·7	Few present
	1	0·002	0·20	1·6	8·5	
	3	0·020*	0·17	1·7	7·5	
	5	0·003	0·15	0·1	6·0	Maximum large
Esthwaite	12	0·0022	0·14	2·4	15·7	Few present
	1	0·002	0·085	1·7	15·5	
	3	0·007	0·14	0·2	12·5	Large maximum
Range of values:						
Minimum		0·002	0·060	0·8	6·0	
Maximum		0·020*	0·200	2·4	15·7	

* Actual figure 0·04—but 0·02 used as possibly more accurate (see Part I).

In regard to the second problem which has been suggested, the normal disappearance of diatoms in early summer, it may be pointed out that the most obvious effect of diatom growth upon the dissolved substances is the early removal of silica, a feature which is not observed in Wastwater and Ennerdale where diatoms are practically absent. The depletion of silica in the diatom lake water is relatively much more rapid than that of nitrate and phosphate. In Esthwaite, for example, an enormous *Asterionella* maximum in March caused the silica to fall from 1·7 to 0·2 mg. per litre. Diatoms persisted until May in small numbers but high proportions, the silica falling further to 0·1 mg. In five lakes (Esthwaite, Windermere, Lowes Water, Derwentwater and Bassenthwaite) the sequence is essentially the same and the disappearance of the spring diatoms is associated with a fall in silica to below about 0·5 mg. per litre. In Ullswater, with diatoms dominant all the year round, silica does not fall below this level in summer. It seems probable then that large maxima of diatoms or substantial increases in the proportions of diatoms will not take place in these lakes if silica is below 0·5 mg. per litre.

The chief complication in the data arises from the method of presentation. In Esthwaite (May), Windermere (June), Bassenthwaite (July), the figures show high *proportions* of diatoms. In each case, there had been a very large diatom maximum at the preceding collection and the quantity of phytoplankton had fallen very low in the subsequent collection—though no other organism had succeeded in replacing the diatoms which had thus persisted as dominants. These examples illustrate very clearly the weakness of the method of enumeration employed.

It should be clearly recognised that silica cannot be the *only* factor involved in the production of diatom maxima. In the example quoted of Esthwaite, silica is above the suggested limit from June onwards. Though the diatom proportions at first increase, they become very low from August onwards, even during the general rise in nutritive substances during November and December. Some other factor (or factors) is clearly involved, and probably it is connected with the successful competition of Myxophyceae. Further, in those lakes with low calcium content (Wastwater, Ennerdale, Crummock), the silica is always high. In Crummock, diatoms are only abundant following periods when the calcium carbonate is above 3·0. In the Ennerdale this figure was never reached, and in Wastwater it was attained only in January, and in the following month a little *Tabellaria fenestrata* was observed, though the numbers were very small. In Derwentwater the disappearance of diatoms in May was correlated with a fall in both silica and calcium carbonate to the lower limits. In general, therefore, the diatoms only appear to be abundant when the calcium carbonate is above 3·0, estimated as carbonate hardness.

TYPES OF DIATOM PERIODICITY.

It may be convenient to summarise at this stage the different kinds of diatom periodicity in the various lakes in 1928.

I. In Wastwater and Ennerdale—no definite diatom maximum existed. This feature appears to be associated with the low calcium content of the water. The winter period, from December to May, was characterised by a stage when a few diatoms like *Tabellaria flocculosa* were almost the only living organism present. It was impossible to describe this as a true phytoplankton. The Wests (**4**) found *Rhizosolenia morsa* present in fair numbers at this time. This diatom was not observed at all in Wastwater during 1921, 1922 and 1928, and of these three years, 1928 was the only one in which it appeared in Ennerdale, and even then only isolated examples were seen (see **3**).

II. The second class of lake, including Derwentwater, Bassenthwaite and Ullswater as examples, comprised the waters in which *Tabellaria fenestrata* and *Asterionella* were prominent. The three examples named differed, however, in the nature of the spring plankton maximum in June. In Derwentwater, this was composed of *Dinobryon divergens*, in Bassenthwaite of *Tabellaria fenestrata*, and in Ullswater of *Asterionella formosa*. In each case this maximum started to develop after March and it is, therefore, possible to compare the water analyses in March, May and June in order to contrast the conditions under which the three organisms named above can rapidly develop.

Table II.

		Phosphate P	Nitrate N	CaCO₃	SiO₂	
Derwentwater	III	0·007	0·055	3·0	0·9	
	V	0·0035	0·055	0·5	0·4	*Dinobryon*
	VI	0·002	0·050	4·0	0·4	
Bassenthwaite	III	0·005	0·085	7·0	1·7	
	V	0·0025	0·085	5·0	0·7	*Tabellaria*
	VI	0·001	0·100	8·5	0·1	
Ullswater	III	0·010	0·085	11·0	2·2	
	V	0·004	0·075	8·0	1·0	*Asterionella*
	VI	0·002	0·080	12·5	0·5	

Derwentwater clearly stood alone in its deficient silica and its lower nitrate. Calcium was not generally much lower than that of Bassenthwaite—after correcting (see Part I, This JOURN. **18**, p. 310) by adding 2·5 to the figures given—although the low value in May was associated with the practical disappearance of diatoms. It seems probable then that low SiO₂ and calcium were the cause of diatoms being scarce and of *Dinobryon* replacing them. Contrasting Bassenthwaite and Ullswater, we may comment upon the generally higher level of phosphate and silica in Ullswater. The difference is very striking in the case of phosphate, and it seems probable that it is this which favours the development of *Asterionella* in Ullswater. In agreement, examination of the analyses shows that this diatom becomes most abundant in Ullswater when the N/P ratio is lowest (see Fig. 1).
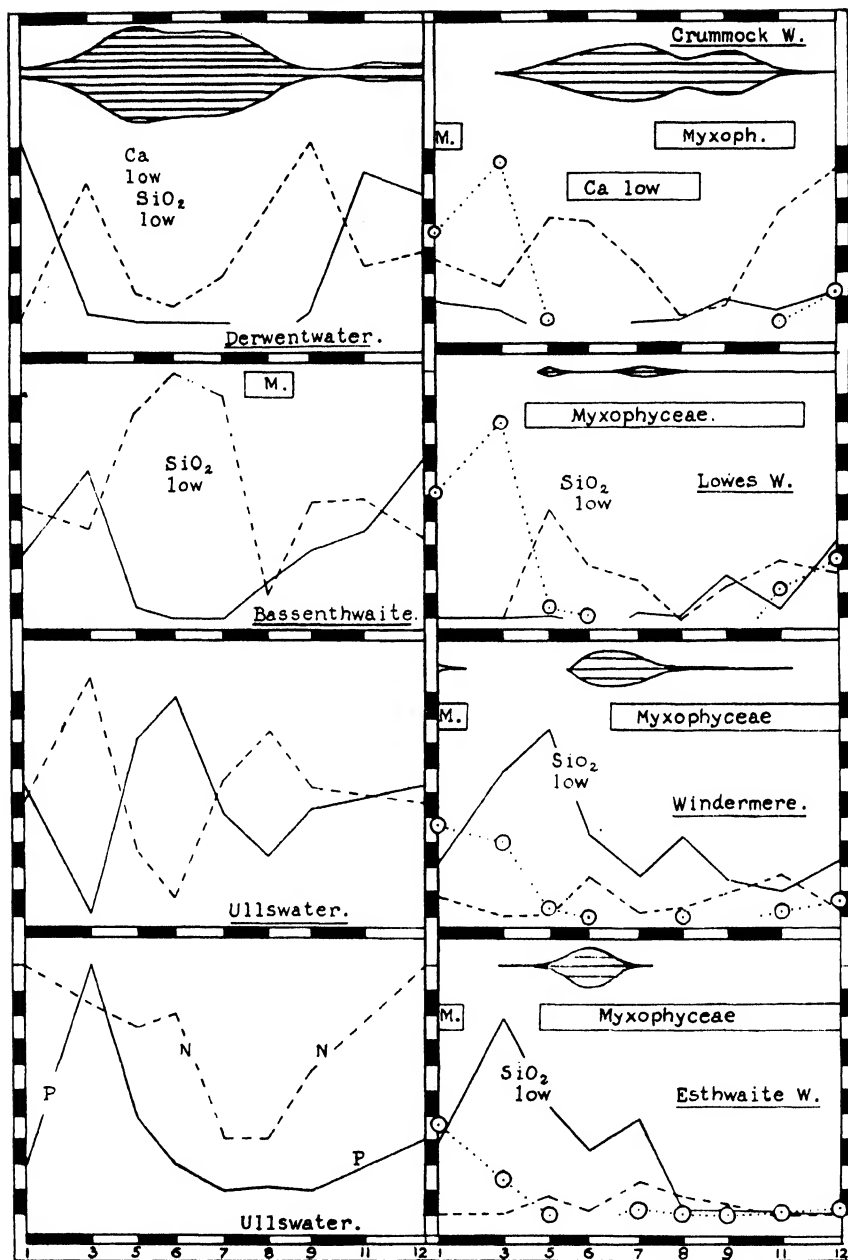
Fig. 1. Types of diatom periodicity in different lakes (1928). Prominent species as percentages of total phytoplankton, the vertical scales showing units of 10 per cent. *Asterionella*—continuous lines; *Tabellaria fenestrata*—broken lines; *Melosira granulata*—circles and dotted lines; *Dinobryon divergens*—shade areas (half scale). There are also shown the times (1) when Myxophyceae (M.) made up more than 20 per cent. of the total algae; (2) when calcium (Ca) and silica (SiO_2) were below the assumed limits for abundant diatoms. The bottom left hand graph gives curves for nitrate (N) and phosphate (P) showing how *Asterionella* follows high proportions of phosphate. The P scale is ten times larger than the N scale.

III. The third type of diatom periodicity is that characteristic of lakes possessing an abundance of Myxophyceae. Its peculiarity is that *Melosira granulata* is abundant in the period from January to March. Four lakes have these features in common, namely Crummock, Lowes Water, Windermere and Esthwaite. An examination of the figures shows that they differ somewhat in other details; the two former have *Tabellaria fenestrata* as a second characteristic diatom, while in Windermere and Esthwaite, *Asterionella* ultimately becomes the most important diatom. Analytically, there seems to be no way of distinguishing the *Melosira* lakes as a class except that they normally show higher proportions of organic matter. It is curious that *Melosira* should always disappear after March though silica, phosphate and nitrate are then most abundant. But an examination of the records shows that *in every lake* a change in the dominant organism takes place at this time. Where there is a large *Asterionella* maximum (Windermere and Esthwaite) this is perhaps understandable, if we assume *Asterionella* to be more successful when the nutrient level becomes high. In Crummock and Lowes Water, *Tabellaria fenestrata* temporarily becomes important as *Melosira* vanishes. In each case at this time (May) calcium is too low for *Asterionella*. *Tabellaria* apparently disappears in Crummock because the calcium content becomes too low (June), and in Lowes Water because silica is depleted. Except in Lowes Water where Myxophyceae are prominent at a strikingly early period, *Dinobryon* appears to be the first organism to replace the diatoms and this suggests that it has a generally similar nutrient requirement.

PERIODICITY AND DISTRIBUTION OF *DINOBRYON*.

It is convenient, therefore, to discuss next the factors which may be responsible for the decided *Dinobryon* phase which often occurs in spring or early summer.

Among the English Lakes, Derwentwater is the lake most usually characterised by *Dinobryon*, and in 1928, *D. divergens* made up 75–80 per cent. of a considerable plankton in May and June. The average water conditions during March to June are given in Table III, and these must approach the ideal for *Dinobryon* in this series of lakes. There are, however, in the case of *Dinobryon* two clear types of problem.

(1) *Lakes with a decided spring diatom maximum (and high calcium).*

In these (Lowes Water, Derwentwater, Esthwaite, Windermere), a *Dinobryon* maximum occurred when the SiO_2 content fell below 0·5 mg. per litre. There was, therefore, none in Ullswater where the SiO_2 was always above this figure. In Bassenthwaite (6, 7, 8), *Dinobryon* though always present was never abundant possibly owing to the operation of other factors (see below).

(2) *Lakes with a small or no spring diatom maximum (and low* $CaCO_3$).

In these, falling $CaCO_3$ favoured *Dinobryon* rather than *Tabellaria* (Crummock, 6, 7; Derwentwater, 5). But the presence or absence of *Dinobryon* obviously also depends on other factors, since it did not occur in Ennerdale, where $CaCO_3$ was below the diatom limit but did occur in Wastwater where the $CaCO_3$ was approximately the same. The *Dinobryon* phase in the latter lake developed during June, July and August, and in the following summary is given the average water condition at this time, together with data for the same months in Ennerdale and the conditions in Crummock and Derwentwater when the *Dinobryon* phase was developing.

Table III.

Lakes	Months	Phosphate P	Nitrate N	N/P	Maximum percentage of Dinobryon
Ennerdale	6, 7, 8	0·0026	0·025	9·6	3
Wastwater	6, 7, 8	0·0020	0·048	24·0	30
Crummock	5, 6, 7	0·0028	0·047	16·5	44
Derwentwater	3, 5, 6	0·0026	0·053	20·6	75

These figures certainly suggest that *Dinobryon* requires a high ratio of nitrate to phosphate (N/P). (It cannot be simply a question of high nitrate requirement because when (in Ennerdale, 1–5) the nitrate was actually higher, though N/P was low, no development of *Dinobryon* took place.) In support of this suggestion it should be noted that the end of the *Dinobryon* phase in Derwentwater came in July when nitrates nearly disappeared. Further, on returning to consider the case of the lakes with spring diatom maxima and high calcium content, it appears that in these also *Dinobryon* attains the highest proportions of the plankton where the N/P ratio is high. There is, indeed, a suggestion of proportionality.

Table IV.

Lakes	Months	Phosphate P	Nitrate N	N/P	Maximum percentage of Dinobryon
Esthwaite	5, 6	0·00175	0·120	68·5	36
Windermere	5, 6, 7	0·00260	0·137	53·0	25
Lowes Water	5, 6, 7	0·00166	0·083	50·0	10
Bassenthwaite	6, 7, 8	0·00097	0·045	46·5	3
Ullswater	5, 6, 7	0·00257	0·062	24·0	−1

In the above table the figures for Bassenthwaite refer to the conditions at the end of the diatom phase—in order to maintain the comparison. *Dinobryon* was actually rather more abundant in November, but if the data were taken for this latter period it would not alter the conclusion. While the percentages of *Dinobryon* in Bassenthwaite are too small to be considered of great significance, it is not without interest to note that while *Dinobryon* was present in *every collection* the two small maxima followed the only times when the N/P ratio was exceptionally high. In a similar way the periodicity of *Dinobryon*

in Esthwaite (and to a less extent in Windermere) shows a good correlation with the rise or fall of the N/P ratio, but not with either phosphate or nitrate independently. It is unlikely that these correlations will hold exactly—because other factors (e.g. silica content) are undoubtedly operating beside the N/P ratio, and the general failure of *Dinobryon* to become abundant during the autumn rise in the N/P ratio (September onwards) may, in some cases (as for example in Derwentwater), be correlated with the rise in silica and consequent development of diatoms, or in other cases (like Windermere and Esthwaite) be obviously associated with a failure to compete with Myxophyceae. The causal factors are complex and we can only attempt to work out apparent correlations with a view to further study. There is another disturbing feature in the present case, namely, the large differences in the magnitude of the N/P ratio in the less calcareous lakes as compared with the more calcareous. In the former case, the values are low (6–30)—in the latter case they are high (20–100). The differences are due both to the higher phosphate and the lower nitrate of the less calcareous waters. If the attempt made to trace a connection between these ratios and the incidence of *Dinobryon* is well founded—then it must be supposed that the direct or indirect effects of a higher calcium carbonate content have to be balanced, as it were, by relatively higher supplies of nitrate.

Periodicity and distribution of green algae.

It will be apparent from what has been said already that the summer plankton organisms develop under conditions in which the nutritive and other substances in the water are reduced to their lowest levels, particularly by the effects of the spring diatom maxima. This depletion of the nutrient ions progresses during the summer, reaching its greatest intensity in August and September when the concentrations of nitrate and phosphate are normally lowest. Nitrates and phosphates are not, however, removed at proportionate rates, the nitrates generally disappear more quickly, and they began to rise in 1928 during September. The nitrate/phosphate ratio thus falls during the summer. It is during this period of lower nitrate and phosphate content that the green algae develop. Green organisms are only dominant in Ennerdale and Wastwater. The common characters of these waters are their low calcium contents and relatively high summer phosphate content (see Table V). Both of these characters are shared by Crummock in which *Dinobryon* and Myxophyceae to some extent supplant the green algae. It is suspected that the differences shown by Crummock are associated with its much higher organic content (see Table V).

Apart from these relations the main feature in the periodicity of the green algae is the fluctuation in the proportions of colonial Chlorophyceae and desmids. The former, principally *Sphaerocystis Schroeteri*, are most abundant in the early summer—the desmids tend to replace them in late summer. This

feature is so constant that it seems that the colonial forms may require higher concentrations of nitrate and of phosphate than the desmids.

That this cannot be the only factor is, however, evident from the consideration of the fact that the more calcareous lakes have lower proportions of phosphates in summer (see Table V), yet generally higher proportions of green algae. It must be, therefore, either that the desmids are favoured by lower ratios of nitrate to phosphate or that a higher calcium content of the water disturbs the balance in favour of other green algae. The latter supposition for which there is good evidence will be considered at a later stage. For the present it may be noted that the ratio of nitrate to phosphate (N/P) usually falls during summer (except in Wastwater) and that the green algae (and *Dinobryon*) occur while it is still high, while the desmid maximum develops immediately this ratio falls to its lowest level. It is not easy to discuss in detail the operation of this factor in periodicity, because the actual concentrations of nitrate and of phosphate are falling at the same time. There is, however, another line of enquiry which supports the suggestion made above.

The average summer conditions in the different lakes of the series are markedly dissimilar and these differences seem, broadly, to run parallel to the observed differences in the summer plankton. In the following table are given the average conditions of dissolved solids for the months of June, July and August, which lead up to the general maximum of green forms about August or September.

Table V. *Average analyses for summer,* 1928.

Group	Lake	Fe	Phosphate P	Nitrate N	$CaCO_3$	pH	SiO_2	Albuminoid NH_3*
I.	Ennerdale	0·028	0·0026	0·025	2·0	6·6	1·6	0·038
	Crummock	0·027	0·0026	0·035	2·2	6·9	1·0	0·057
	Wastwater	0·025	0·0020	0·048	2·2	6·9	1·9	0·026
	Derwentwater	0·026	0·0018	0·025	3·7	7·0	0·53	0·035
II *a*.	Bassenthwaite	0·020	0·0010	0·053	8·7	7·3	0·2	0·01–0·04
	Lowes Water	0·017	0·0011	0·054	6·2	6·9	0·4	0·082
	Windermere	0·029	0·0017	0·103	8·8	7·2	0·5	0·075
II *b*.	Ullswater	0·025	0·0014	0·047	11·0	7·3	0·6	0·045
	Esthwaite	0·025	0·0011	0·060	12·7	7·2	0·4	0·070

* June results only. Figures as parts per million.

The classification in this table is based first, on the calcium content of the water and then, in each group, the lakes are arranged in order of ascending nitrate content. Derwentwater is intermediate in character. It could on its carbonate hardness be placed in group I. On the other hand, its calcium content is much higher than is shown by its carbonate hardness and on calcium content it could be included in group II (with Lowes Water) to which group it also belongs biologically in the presence of considerable proportions of diatoms. A comparison may now be made between the results of this table and the average percentage composition of the plankton in July, August and September, 1928.

Table VI.

Group	Lake	Desmids	Green Colonial	*Dinobryon*	Desmids / Colonial	N/P
I.	Ennerdale	76·0	17·0	—	4·5	9·6
	Crummock	11·6	5·5	31·0	2·1	13·5
	Wastwater	39·0	23·0	11·0	1·7	24·0
	Derwentwater	7·5	3·5	39·0	2·1	13·8
II *a*.	Bassenthwaite	13·0	1·5	1·5	8·6	53·0
	Lowes Water	10·5	1·5	4·0	7·0	49·1
	Windermere	7·0	12·0	10·0	0·6	60·6
II *b*.	Ullswater	2·5	0·5	0·5	5·0	33·6
	Esthwaite	2·0	5·5	1·5	0·36	54·5

A comparison of these two tables will show that generally, in each group of lakes, the ratio of desmids to green colonial forms falls as the N/P ratio rises. Derwentwater may clearly be placed along with Crummock in this respect. The ratios of desmids to green colonials are very high in Bassenthwaite and Lowes Water, and while both of these lakes have peculiar features (like peaty water) which may disturb these comparisons, it should be recognised also that the different lakes contain very different species of desmids and to some extent of Chlorophyceae, so that detailed comparison should not be pressed too far.

These differences between the species of desmids in lakes of otherwise similar appearance and biological character are one of the most striking features of the lake planktons. The contrast is very clear in the case of Ennerdale and Wastwater, both with desmids dominant, yet the former with *Staurastrum longispinum* most abundant (in 1928) and the latter with *Staurastrum jaculiferum*. Since Ennerdale is a low nitrate lake and Wastwater has a high N/P ratio, it is worth while analysing the distribution of desmid species to see how far it may be related to this factor. Associated with *Staurastrum longispinum* in this lake area are a number of other rarer species, including *S. anatinum*, *S. Arctiscon*, *S. Brasiliense* var. *Lundellii*, *S. grande*, *S. megacanthum*, *S. Ophiura*, *Genicularia elegans*, *Arthrodesmus Incus* and *A. crassus*, which may be referred to as group I. Associated with *S. jaculiferum* are particularly *S. curvatum* and *S. cuspidatum* var. *maximum* (group II). The way in which these two groups are distributed in the various lakes is shown in the following summary, further details being obtainable from the Appendices. The lakes are arranged as in the preceding tables.

Table VII.

Lake	No. of species Group I	No. of species Group II	Percentages of all desmids Group I	Percentages of all desmids Group II	N/P	Ca
Ennerdale	7	2	75	1	9·6	
Crummock	4	3	13	36	13·5	Low
Wastwater	1	3	2	62	24·0	
Derwentwater	8	0	63	0	13·8	
Bassenthwaite	5	0	11	0	53·0	
Lowes Water	5	2	52	8	49·1	Medium
Windermere	2	3	7	28	60·6	
Ullswater	0	2	0	20	33·6	High
Esthwaite	0	1	0	0	54·5	

The percentages are for the time of the desmid maximum, 1928.

The table indicates very clearly that the first group of desmids is characteristic of the low nitrate lakes, while the second group tends to occur rather where nitrates are more abundant. Derwentwater here occupies a somewhat anomalous position. It contains most of the species of group I in large proportions, and clearly resembles Ennerdale in this rather than any other lake. It would be, however, also in place at the head of the second group of lakes. It is possible that the decisive feature of the summer period in Derwentwater was the extraordinary drop in nitrates in July, when they almost disappeared. This is masked in the average analyses, but it might well determine the biological character of the summer plankton and it would certainly allow a marked contrast to be made with the conditions in Crummock which is otherwise quite similar.

It will be recognised that other factors play a considerable part in determining the species and proportions of desmids present in the lakes. Particularly is this evident in the case of the two most calcareous lakes, in which few of the species under discussion are found. The calcifuge character of many desmids is well known and in this series of lakes the waters have a range of calcium content which seems to be greater than that required by many of the plankton desmids.

The examination of the records suggests that there are in this lake area at least three groups of desmids with differing calcium requirements. In the first group, occurring in waters with a carbonate hardness of less than 7, are *Staurastrum Arctiscon*, *S. Brasiliense* var. *Lundellii*, *S. longispinum*, *Arthrodesmus Incus* and *Genicularia elegans*. Probably *S. Ophiura*, *S. grande*, *S. megacanthum* and *A. crassus* also belong to this group. The following are found in waters of carbonate hardness of less than 10: *Staurastrum anatinum*, *S. jaculiferum*, *S. cuspidatum* var. *maximum*, *S. curvatum*, *Closterium Kutzingii*, *Xanthidium subhastiferum* var. *Murrayi* and *Gonatozygon monotaenium*. The third group, tolerating carbonate hardness up to 13–14, is: *Staurastrum paradoxum*, *S. lunatium* var. *planctonicum*, *Xanthidium subhastiferum* (and its varieties *depauperatum* and *triquetrum*) and *Spondylosium planum*. It is recognised that these limits may be complicated by the operation of other factors such as those already discussed, but the figures given represent a summary, not only of the data of the present papers, but also of the conditions in the other larger and smaller lakes of this district in previous years. Some of the species mentioned, and certainly *Staurastrum paradoxum*, probably grow in much wider range of calcium content than is represented in these lakes. The effects of calcium are not clearly discernible among the other green algae although *Eudorina elegans*, *Volvox* spp., and *Tetraspora lacustris* seem to be more characteristic of the waters with higher calcium content (carbonate hardness + 6·0).

A further point about the desmids is that they are often associated with peaty waters. In this lake area there is no definite correlation between peaty

water and desmids. It is true that Bassenthwaite and Lowes Water, each with peaty water, have high ratios of desmids to other green algae, but Esthwaite is equally peaty and has fewer desmids than any other lake, probably because of its high calcium content, while Crummock Water, also slightly peaty, has no exceptional proportion of desmids. The lakes, like Ennerdale and Wastwater, with a striking desmid plankton, are those with the clearest and least coloured waters. Further, it has already been noted (Pearsall (2)) that the analyses of the Rivers Pollution Commission show no evidence of peaty organic matter in any of these lakes in summer, while the organic content of the lake waters is usually, though not necessarily, low in the best desmid lakes. Finally, the differences in hydrogen-ion concentration of the lake waters are small and no influence due to acid peat can be detected. It seems somewhat doubtful, therefore, on the present evidence, whether peat can have any direct influence on the desmid plankton. It may be suggested that the connection is indirect, because areas of acid peat are usually both very poor in calcium and in nitrates and both of these factors have been shown to favour the appearance both of the rarer desmids and of desmids in general in this lake area.

Recent work has suggested the probability that the organic matter present in lake waters may be of direct nutritive importance. In the English Lakes, however, there seems to be little correlation in general between the green algae and the amount of organic matter present in summer. It may be worth noting, however, that *Eudorina elegans* is particularly abundant in the more organic waters of Esthwaite, Windermere and Lowes Water, whilst *Volvox aureus* is confined to these lakes. Similarly *Staurastrum paradoxum* is particularly characteristic of these lakes and of Crummock with a slightly lower organic content, and inconspicuous or absent in the others. In 1928, it appeared in abundance in Bassenthwaite where it had previously been scarce, and its appearance in August coincided with an exceptionally high content of organic matter. The albuminoid ammonia rose to 0·077 parts per million as contrasted with a normal value of 0·01-0·04. There seem to be grounds, therefore, for associating this form with high organic matter. *Spondylosium planum* also appeared abundantly in Bassenthwaite in August, and as its distribution is also chiefly in the more organic lakes it may also be favoured by high organic matter. The data are insufficient to warrant further comment.

There is another group of green algae which, in distribution and periodicity show some points of interest. This group is represented chiefly by *Tetraspora lacustris*, and *Dictyosphaerium pulchellum*, but apparently possessing similar affinities are *Tetraspora limnetica* and *Volvox aureus*. These differ from the more generally distributed green algae in occurring much later in the year, and in reaching a maximum about August or September. They are also characteristic of the more calcareous lakes (particularly Windermere and Esthwaite). The water conditions during the period of their development are sufficiently contrasted as follows:

Table VIII.

	Phosphate P	Nitrate N	CaCO$_3$
I. Three lakes, *Sphaerocystis* and *Gleocystis* only	0·00240	0·036	2·15
II. Five lakes*, *Tetraspora* and *Dictyosphaerium* also	0·00126	0·063	9·50

(Average conditions for June to August.)

* Excluding Ullswater.

These species to some extent replace the desmids in lakes with higher calcium, lower phosphate and high N/P ratios.

Finally, brief reference should be made to the peculiar periodicity of *Closterium Kutzingii*, a desmid which develops in winter, along with the diatoms and which reaches its maximum about April or May, after which it disappears. Although it is absent or scarce in the most calcareous lakes, it seems otherwise to require the same habitat conditions as the diatoms.

The detailed examination of the evidence shows, therefore, that the green algae occur during the period when the concentrations of nitrates and phosphates in the waters are low, and that their distribution and periodicity is also affected by the ratio of nitrate to phosphate and the calcium content of the water. In general, a low N/P ratio and a low calcium content are likely to favour desmids.

MYXOPHYCEAE.

The blue-green algae are the last group of plankton forms to be considered because, so far as it can be ascertained, they seem to have somewhat different requirements from the more generally distributed groups. The two chief forms are *Oscillatoria tenuis* and *Coelosphaerium Kutzingianum*. The figures given in the Appendix show two main types of periodicity in 1928 (which have been observed previously). In Crummock and Lowes Water the maximum comes about August, while in Windermere and Esthwaite the blue-green algae become increasingly abundant until about November and December. These differences cannot be attributed to temperature or to the physical differences of the lakes. Lowes Water and Esthwaite are very similar in configuration and depth, and Crummock and Windermere are both deep lakes. It seems possible, however, that the differences are related to the variations in the organic content of the lake waters. The first argument in favour of this is that in 1928 the proportions of Myxophyceae in the plankton of the various lakes in July closely followed the amount of albuminoid ammonia present in June and July. The following summary gives the albuminoid ammonia for June and the July figures for Bassenthwaite and Windermere, where there was a marked change in this character, and also the percentage of Myxophyceae in the plankton in the following month, July, and for August also in the case of Windermere and Bassenthwaite.

Table IX.

	Bass.	Wast.	Derw.	Ennerd.	Ullsw.	Crum.
Albuminoid NH$_3$ in June	0·010	0·026	0·035	0·038	0·045	0·057
Percentage of Myxophyceae in July	0	0	3	7	2	19

	Wind.	Esthw.	Wind.	Bass.*	Lowes
Albuminoid NH$_3$ in June	0·061	0·070	0·075	0·080	0·082
Percentage of Myxophyceae in July	26	27	46	51	61

* July (Alb. NH$_3$) and August (plankton).

The data show very clearly the correlation between organic matter and Myxophyceae. The figures for Windermere give a decrease in albuminoid ammonia in July followed by a reduction in Myxophyceae. The Bassenthwaite figures are particularly striking, as this lake has never previously been observed with a large Myxophycean element in the plankton. The sequence of events was that an enormous diatom maximum in May and June was dying away. The organic matter rose from a minimum figure (0·01) to an extremely high one (0·077), the usual figure for this lake in summer being 0·03–0·04. The high organic content was followed by the abnormal development of *Oscillatoria* in considerable numbers. This sequence at once suggests that the organic matter is one of the determining factors in the production of Myxophycean maxima and also that the decay of the spring diatom maxima may have much to do with the rise of organic matter in early summer, and therefore with the summer production of abundant Myxophyceae.

Returning now to the two types of Myxophycean periodicity distinguished in these lakes, it may be noted that in Ennerdale, where the water conditions are very similar to those of Crummock, the maximum of albuminoid ammonia occurs in the period of July to October (1). It is reasonable to suppose that similar changes occur in Crummock when the Myxophyceae reach their maximum. Lowes Water, lying among similar hills and draining into Crummock, is probably similar, especially as this lake had an enormous diatom maximum in March immediately preceding the very early appearance of numerous Myxophyceae. It is curious that in Esthwaite, where there was also an exceptionally large diatom maximum, and where physical conditions closely resemble those of Lowes Water, the Myxophyceae become dominant very slowly until they practically replace everything else by December. Windermere was similarly late. Although only isolated data are available, it appears that the maximum organic content of these waters usually develops during late autumn, after the leaf-fall, and this would agree with the comparatively late Myxophycean maximum. It should be remembered in this connection that these lakes have drainage systems with comparatively deep soil and a vegetation which is luxuriant compared with that surrounding Crummock and Lowes Water. The autumnal decay of vegetation has undoubtedly much more pronounced effects upon the lake waters in the former cases.

Lastly, the striking absence of Myxophyceae in spring when the organic content of the waters is at a minimum clearly agrees with the assumption that these algae are intimately dependent on the organic content of the waters.

There are considerable differences in the distribution of the commoner forms of Myxophyceae, well illustrated by *Oscillatoria tenuis* and *Coelosphaerium Kutzingianum*. The former only occurs abundantly in three of the more calcareous lakes, Bassenthwaite, Windermere and Esthwaite. *Coelosphaerium*, however, is also dominant in Crummock and Lowes Water, and it occurs as the chief blue-green form in Wastwater and Ennerdale, though never abundantly. These latter lakes are all much less calcareous. It seems probable, therefore, that *Oscillatoria* has a· higher calcium requirement than *Coelosphaerium*, and it occurs here in abundance only when the carbonate hardness is above 7 or 8. The species of *Anabaena* (viz. *A. flos-aquae, A. Lemmermannii, A. circinalis*) did not in 1928 play any important part in the Myxophycean periodicity, except in Esthwaite where there was an August maximum of *A. Lemmermannii* and *A. flos-aquae* of moderate size. In Lowes Water there was a smaller maximum of *A. circinalis* in July. *Anabaena* is usually more characteristic of the smaller and shallower lakes in this area, especially Esthwaite, Lowes Water and Derwentwater, but it is often well represented in Windermere which is large and relatively deep. No evident relation to the water conditions has been detected.

Taking the Myxophyceae as a whole, it seems clear that their habitat requirements are much different from those of the Chlorophyceae, though like the latter they can develop in abundance when the dissolved nitrates and phosphates are at a low level. Since they may also occur abundantly during the autumnal rise of these substances, it is hardly likely that their appearance is limited by the falling nitrate and/or phosphate content in early summer. Their distribution and periodicity thus seems to be largely independent of the factors affecting the other groups of algae. Further, when they show a definite autumnal maximum (e.g. Esthwaite and Windermere) they delay the appearance of diatoms, although the water conditions may appear to be otherwise very suitable for diatoms. Given the special conditions they require, the Myxophyceae thus seem to be a dominant and highly efficient group.

It will thus be evident that there are quite definite correlations between the proportionate distribution and periodicity of the plankton algae types and the quality and seasonal changes of the dissolved substances. It must remain for future work to say whether these correlations indicate a true causal connection.

SUMMARY.

By analysing the periodicity of the more important plankton algae in comparison with the results of water analyses, it appears that:

(1) Diatoms occur when the waters are richest in nitrate, phosphate and silica (in winter and spring). The appearance of *Asterionella* is correlated with

higher concentrations of phosphate, nitrate and calcium than that of *Tabellaria fenestrata*. *Melosira granulata* shows a very definite correlation with waters rich in organic matter and in Myxophyceae, and forms maxima in water of low calcium content.

(2) The green algae and desmids occur in summer when nitrates and phosphates are low. Two groups of green colonial forms are distinguished, occurring before and after the desmid phase. Desmids occur particularly when calcium and the nitrate/phosphate ratio is low. No evident effect of peaty water is detected.

(3) *Dinobryon* appears to be favoured by somewhat higher ratios of nitrate to phosphate. It may replace diatoms when the silica or calcium content gets low in spring.

(4) Myxophyceae show a general correlation with high organic matter, and have the ability to grow rapidly in minimal quantities of nitrate and phosphate. *Oscillatoria tenuis* has apparently a higher calcium requirement than *Coelosphaerium Kutzingianum*.

REFERENCES.

(1) **Pearsall, W. H.** "Phytoplankton in the English lakes. I. The proportions in the waters of some dissolved substances of biological importance." This JOURN. **18**, 306, 1930.

(2) **Pearsall, W. H.** "Phytoplankton and environment in the English lakes." *Rev. Algologique*, **1**, 1, 1924.

(3) **Pearsall, W. H.** and **W. Harrison.** "The phytoplankton of the English lakes." *Journ. Linn. Soc. (Bot.)*, **47**, 55, 1925.

(4) **West, W.** and **G. S.** "On the periodicity of the phytoplankton of some British lakes." *Journ. Linn. Soc. (Bot.)*, **40**, 227, 1912.

APPENDIX.

The following tables show the periodicity of the more important algae in the plankton. A plus sign indicates that the alga was present, a number shows the proportion present expressed as a percentage of the whole phytoplankton. No numbers are given in cases where the plankton algae as a whole were very scarce.

Wastwater.

Date:	31.i	24.iii	5.v	1.vi	10.vii	16.viii	20.ix	3.xi	20.xii
Mougeotia spp.	+	+	+	36	26	1	17	26	17
Gonatozygon monotaenium	.	.	.	+	3	9	19	14	.
Staurastrum jaculiferum	.	.	.	5	6	22	34	36	10
S. Arctiscon	.	.	.	.	.	.	+	+	+
Sphaerocystis Schroeteri	+	.	.	.	.	14	+	+	.
Gleocystis gigas	.	.	+	+	6	5	12	.	.
Dinobryon divergens	.	.	.	+	3	30	.	.	.
Tabellaria flocculosa	.	+	+	9	9	12	5	.	.
Totals:									
Colonial greens	+	+	+	9	31	25	14	8	3
Desmids	+	+	+	18	25	32	59	70	60
Diatoms	+	+	+	15	15	6	6	3	11

Ennerdale Lake.

	Date:	31.i	24.iii	5.v	1.vi	10.vii	16.viii	20.ix	3.xi	20.xii
Gonatozygon monotaenium	...	+	.	.	.	5	41	15	18	35
Genicularia elegans ...	...	+	+	+	+	7	8	2	7	6
Closterium Kutzingii ...	... •	+	+	+	.	.	.	.	.	+
Arthrodesmus Incus ...	...	.	+	+	29	5	4	+	.	.
Staurastrum anatinum	...	.	.	+	3	+	1	+	+	.
S. Arctiscon ...	...	+	.	+	1	5	+	5	+	.
S. brasiliense ...	...	+	.	+	7	5	12	10	.	.
S. jaculiferum ...	...	.	.	.	+	+	+	+	.	.
S. longispinum ...	...	+	+	+	22	6	8	57	13	4
Sphaerocystis Schroeteri	...	.	.	+	+	5	+	.	.	.
Gleocystis gigas	...	+	+	+	2	5	2	+	.	.
Tabellaria flocculosa ...	...	+	+	+	+	.	.	.	.	.
T. fenestrata ...	...	+	+	+	2	11	.	.	.	8
Cyclotella compta ...	...	+	+	.	+	.	+	.	.	+
Rhizosolenia morsa ...	...•	.	+	+	+	.	.	.	.	.
Dinobryon spp. ...	...	.	+	+	+	+	+	.	.	.
Totals:										
Colonial greens ...	...	+	+	+	12	29	21	+	2	1
Desmids ...	...	+	+	+	78	52	75	99	91	76
Diatoms ...	...	+	+	+	4	12	1	+	7	17
Blue-greens ...	...	+	.	.	2	.	1	.	+	6

Crummock Water.

	Date:	31.i	24.iii	5.v	1.vi	10.vii	16.viii	20.ix	3.xi	20.xii
Closterium Kutzingii ...	...	+	+	3	.	.	.	.	.	2
Xanthidium antilopeum	...	.	.	+	+	1	+	+	.	+
Staurastrum anatinum	...	+	+	+	+	1	2	+	+	1
S. Arctiscon ...	...	.	+	.	+	.	+	+	+	.
S. cuspidatum ...	...	.	.	+	+	+	+	.	+
S. jaculiferum ...	...	+	1	4	+	1	4	4	2	2
S. lunatum ...	...	.	+	1	3	2	2	+	+	+
S. paradoxum ...	...	.	+	+	.	+	+	+	1	1
Spondylosium planum	...	+	+	5	6	1	3	3	1	+
Eudorina elegans ...	...	.	.	+	1	1	.	1	.	.
Sphaerocystis Schroeteri	...	.	1	7	2	1	+	+	+	.
Gleocystis gigas	...	.	+	+	1	1	+	+	.	.
Botryococcus Braunii ...	...	+	+	+	2	2	4	+	+	.
Melosira granulata ...	...	36	64	1	.	.	.	.	+	12
Asterionella gracillima	...	8	5	.	.	+	1	9	5	12
Tabellaria fenestrata ...	...	25	15	42	40	23	2	7	45	61
Dinobryon divergens ...	...	.	+	20	38	44	28	35	7	+
Coelosphaerium Kutzingianum		22	6	10	3	17	48	28	26	6
Peridinium Willei ...	...	.	.	+	3	+	+	+	.	.
Ceratium hirundinella	...	.	.	.	.	3	1	6	+	.
Totals:										
Colonial greens ...	...	1	+	9	6	10	4	3	3	1
Desmids ...	...	4	4	13	10	9	15	11	8	7
Diatoms ...	...	69	86	42	40	14	4	17	52	86
Blue-greens ...	...	26	7	10	3	19	48	28	30	6

Lowes Water.

	Date:	31.i	24.iii	5.v	1.vi	10.vii	16.viii	20.ix	3.xi	20.xii
Gonatozygon monotaenium	...	.	.	.	.	1	2	1	+	.
Closterium Kutzingii ...	...	+	+	+	.	.	.	.	+	+
Arthrodesmus Incus ...	...	+	+	2	+	1	.	.	.	+
Staurastrum anatinum	...	.	.	+	+	+	6	5	13	2
S. lunatum ...	...	+	+	+	+	1	1	+	+	+
S. paradoxum ...	...	.	.	.	.	+	.	+	1	2
S. megacanthum ...	...	.	.	.	.	+	+	1	3	3
Spondylosium planum	...	.	1	4	+	+	1	1	+	.

	Date:	31.i	24.iii	5.v	1.vi	10.vii	16.viii	20.ix	3.xi	20.xii
Eudorina elegans		.	+	+	3	2	.	.	+	.
Sphaerocystis Schroeteri		.	.	+	2	+	.	.	+	.
Tetraspora lacustris		+	+	.	.	.	+	+	.	.
Gleocystis gigas		.	.	.	.	+	+	+	+	+
Melosira granulata		51	80	4	2	.	.	.	12	24
Asterionella gracillima		+	+	1	.	2	1	17	4	32
Tabellaria fenestrata		+	+	44	22	16	+	13	23	19
Anaboena spp.		.	4	4	1	10	1	+	+	.
Oscillatoria tenuis		.	.	+	+	.	+	2	+	.
Coelosphaerium Kutzingianum		+	4	32	67	51	74	52	36	15
Dinobryon divergens		.	.	6	+	10	3	1	+	+
Ceratium hirundinella		.	+	+	.	2	4	.	.	.
Totals:										
Colonial greens		1	3	3	5	4	+	+	1	+
Desmids		8	7	6	2	5	14	12	19	9
Diatoms		79	82	49	24	18	3	31	40	75
Blue-greens		10	8	36	69	61	76	56	39	15

Derwentwater.

	Date:	31.i	24.iii	5.v	1.vi	10.vii	16.viii	20.ix	3.xi	20.xii
Closterium Kutzingii		+	+	+	.	.	.	.	+	+
Micrasterias radiata		.	.	+	.	+	1	+	+	.
Xanthidium antilopeum		.	.	.	+	+	+	+	.	.
Arthrodesmus Incus		.	+	4	1	+	+	+	1	.
Staurastrum Arctiscon		+	.	.	+	+	+	+	+	.
S. brasiliense		+	.	.	+	+	+	+	.	.
S. grande		.	.	.	+	+	+	+	+	.
S. longispinum		+	.	.	+	+	+	+	+	.
S. Ophiura		+	.	.	+	+	+	+	+	+
Spondylosium planum		+	+	+	1	+	1	+	1	+
Eudorina elegans		+	+	+	1	+	1	+	1	.
Sphaerocystis Schroeteri		.	.	+	+	2	+	+	+	+
Tetraspora lacustris		+	.	.	.	.	1	+	2	.
Gleocystis gigas		+	.	+	+	+	+	+	+	.
Botryococcus Braunii		+	.	.	+	+	+	+	.	.
Asterionella gracillima		72	3	1	1	+	.	4	60	52
Tabellaria fenestrata		2	56	11	6	18	47	72	22	28
Cyclotella compta		.	+	+	1	+	+	3	+	.
Rhizosolenia morsa		.	+	+	3	.	.	.	+	.
Anaboena spp.		+	.	+	+	1	1	1	+	+
Oscillatoria tenuis		+	.	+	+	2	1	1	+	.
Dinobryon divergens		9	34	80	75	71	39	7	11	11
Ceratium hirundinella		.	+	3	3	1	1	4	+	.
Totals:										
Colonial green		1	+	+	2	4	4	4	3	1
Desmids		8	2	4	8	3	6	4	3	3
Diatoms		77	63	12	12	18	48	77	82	82
Blue-greens		4	+	+	+	3	3	2	+	3

Bassenthwaite Lake.

	Date:	31.i	24.iii	5.v	1.vi	10.vii	16.viii	20.ix.	3.xi	20.xii
Closterium Kutzingii		+	+	.	.	.	.	.	+	+
Micrasterias rotata		+	.	+	.	+	5	+	+	.
M. Wallichii var. Mahabulesh-warensis		4	.	.	+	+	2	+	.	.
Xanthidium antilopeum		.	.	.	+	+	+	+	+	.
Staurastrum anatinum		+	.	+	+	+	+	2	.	.
S. lunatum		.	.	+	+	+	.	+	.	.
S. paradoxum		.	.	.	.	.	2	3	1	+
Spondylosium planum		+	+	+	+	+	8	8	1	+

	Date:	31.i	24.iii	5.v	1.vi	10.vii	16.viii	20.ix	3.xi	20.xii
Eudorina elegans		+	.	.	.	+	.	+	+	.
Sphaerocystis Schroeteri		.	.	+	+	+	+	1	1	.
Asterionella gracillima		26	60	5	+	+	15	27	35	64
Tabellaria fenestrata		45	37	83	99	90	10	47	48	32
Oscillatoria tenuis		.	.	.	.	1	51	5	.	.
Dinobryon spp.		2	+	+	+	3	1	2	4	+
Totals:										
Colonial greens		1	+	2	+	+	2	3	1	+
Desmids		11	1	9	+	5	20	14	3	1
Diatoms		76	98	86	100	92	25	76	91	97
Blue-greens		10	.	+	.	+	51	5	+	+

Windermere.

	Date:	31.i	24.iii	5.v	1.vi	10.vii	18.viii	20.ix	3.xi	20.xii
Xanthidium subhastiferum		.	.	.	.	+	1	+	+	+
Staurastrum curvatum		.	.	.	.	+	2	+	.	+
S. jaculiferum		+	.	+	+	+	1	+	1	1
S. lunatum		.	.	.	.	+	+	+	+	.
S. paradoxum		+	+	+	+	1	5	1	1	1
Spondylosium planum		+	.	+	+	+	1	+	+	.
Eudorina elegans		+	.	.	.	1	3	+	2	.
Volvox aureus		.	.	.	+	.	+	+	2	.
Dictyosphaerium pulchellum		+	.	+	.	+	+	3	+	+
Sphaerocystis Schroeteri		+	+	10	7	3	+	+	1	.
Tetraspora lacustris		+	.	.	.	1	3	15	+	.
T. limnetica		.	.	.	.	.	6	1	.	.
Gleocystis gigas		.	+	+	+	+	+	+	.	.
Botryococcus Braunii		+	+	+	.	.	.	.	+	.
Melosira granulata		37	30	3	+	.	+	.	2	6
Asterionella gracillima		21	59	76	33	17	32	15	10	22
Tabellaria fenestrata		8	+	1	16	2	4	10	17	3
Cyclotella compta		+	+	+	.	.	4	+	.	.
Rhizosolenia morsa		1	5	+	.	.	2	.	.	.
Anaboena spp.		+	.	+	+	2	1	1	2	.
Oscillatoria tenuis		4	3	+	+	28	9	14	14	27
Coelosphaerium Kutzingianum		18	1	2	+	16	16	27	42	37
Dinobryon divergens		2	.	.	24	25	2	3	1	.
Peridinium Willei		.	.	+	+	+	+	.	.	.
Ceratium hirundinella		.	+	+	1	+	5	4	.	.
Totals:										
Colonial greens		1	+	14	10	3	12	20	7	+
Desmids		6	+	1	2	6	11	4	4	2
Diatoms		67	95	82	56	20	44	26	29	33
Blue-greens		24	4	3	5	46	26	44	58	64

Ullswater.

	Date:	30.i	20.iii	5.v	1.vi	10.vii	16.viii	20.ix	21.xii
Xanthidium antilopeum		+	.	+	+	+	+	+	+
Staurastrum jaculiferum		.	.	.	+	+	+	+	+
S. cuspidatum		+	.	.	.	.	.	+	+
Sphaerocystis Schroeteri		.	.	.	1	+	.	.	.
Asterionella gracillima		53	3	72	88	42	25	43	53
Tabellaria fenestrata		46	96	27	8	55	74	52	46
Cyclotella compta		.	+	1	2	1	+	2	.

Esthwaite Water.

	Date:	31.i	24.iii	5.v	1.vi	10.vii	16.viii	20.ix	3.xi	20.xii
Staurastrum paradoxum	...	.	+	+	+	+	1	+	.	.
Spondylosium planum	...	+	+	+	2	2	+	+	+	.
Volvox aureus	... ...	.	.	.	.	+	+	+	.	.
Eudorina elegans	... ...	1	+	+	+	+	3	+	+	.
Dictyosphaerium pulchellum	...	.	.	+	.	1	+	+	+	.
Sphaerocystis Schroeteri	...	.	+	+	7	+	.	.	.	.
Tetraspora lacustris	... ...	.	.	.	.	.	5	+	.	.
Gleocystis gigas	... ...	.	.	.	+	+	1	.	.	.
Melosira granulata	... ...	37	14	+	.	2	+	+	1	2
Asterionella gracillima	...	29	79	43	26	38	2	2	1	1
Tabellaria fenestrata	... ...	+	+	7	2	13	7	4	+	1
Rhizosolenia morsa	... ...	+	3	.	.	.	.	7	+	1
Cyclotella compta	... ...	+	2	4	.	.	.	.	.	+
Anabaena spp.	... ...	+	+	+	6	2	22	4	+	.
Oscillatoria tenuis	... ...	+	+	17	8	3	4	32	54	73
Coelosphaerium Kutzingianum		25	1	3	9	21	38	41	40	6
Aphanizomenon flos-aquae	...	7	.	.	.	.	+	+	.	14
Dinobryon divergens	... ...	.	+	6	36	4	.	.	+	.
Peridinium Willei	... ...	.	.	+	+	+	+	.	.	.
Ceratium hirundinella	... ...	.	+	3	1	9	2	1	.	.
Mallomonas longiseta	... ...	.	.	.	.	+	.	+	+	+
Totals:										
Colonial greens	... ...	+	+	4	7	3	12	2	+	+
Desmids	... ...	+	+	1	3	4	1	1	+	+
Diatoms	... ...	66	98	56	28	53	9	14	3	6
Blue-greens	... ...	33	2	20	23	27	76	82	95	3

THE DRY SEASON IN THE GOLD COAST AND ITS RELATION TO THE CULTIVATION OF CACAO

By A. S. THOMAS.

THE INFLUENCE OF RAINFALL ON VEGETATION.

IT has often been remarked that it is strange that the Gold Coast, the country which is the largest producer of cacao in the world, should have an average annual rainfall less than that of any other region where cacao is a major crop. The contrast between the climatic conditions of this country, and those of the habitat of wild cacao in Surinam (1), renders it surprising that the crop should grow at all. Undoubtedly water supply, or rather its converse—drought—is the most important factor limiting the cultivation of cacao in the Gold Coast.

Chipp (2, 3), in discussing the relationship of climate to vegetation in the Gold Coast, has suggested that for the consideration of the effect of rainfall, not only the total annual rainfall, but also the number of wet days, must be taken into account, and has shown that on the basis of these two factors the Gold Coast may be divided into climatic zones corresponding approximately to the zones of natural vegetation.

This method of classification of stations according to "degrees of wetness" has been utilised also by Auchinleck (4) and Chamney (5), who have included many more stations in their diagrams.

But although these diagrams illustrate a definite relation between the "degree of wetness" and the type of vegetation, yet they present certain anomalous features. Climatically, Kintampo appears to be among the wetter stations, yet floristically it is now in the dry Sudanese (savannah and savannah forest) zone, while Nsawam, which according to the "degree of wetness" is classed in the Sundanese zone, in actual fact is situated within one of the most important cacao-growing areas of the country.

The table compiled by Adams to show the "degrees of wetness," i.e. $\dfrac{\text{inches of rain} \times \text{number of rainy days}}{100}$, for the various stations during 1928 and 1929 (6) also exhibits these inconsistencies. For example, in 1928 Kintampo and Keta Krachi, both in the Sudanese zone, had "degrees of wetness" of 105 and 79 respectively, while Otrokpe and Nsawam, which are in important cacao-producing areas, had "degrees of wetness" of 29 and 24; similarly in 1929 the figures for these four stations were 63, 99, 24, and 17 respectively.

THE IMPORTANCE OF THE DRY SEASON.

In Table I are shown the "degrees of wetness" of stations in the Gold Coast. This table comprises:

(1) "Degree of wetness" of each month, i.e.

$$\frac{\text{inches of rain} \times \text{number of rainy days}}{10}$$

(a rainy day being defined as a day on which is recorded 0·01 inch or more of rain).

(2) "Degree of wetness" of the whole year, i.e.

$$\frac{\text{annual rainfall in inches} \times \text{total number of rainy days}}{100}.$$

(3) "Degree of wetness" of the four dry months, November, December, January, February, i.e.

$$\frac{\text{inches of rain} \times \text{number of rainy days}}{10}.$$

The results embodied in this table are the averages for the five years 1926–30 inclusive; those in the last column are the average of the dry seasons, November to February, of 1926–7, 1927–8, 1928–9, 1929–30. Five years is too short an interval on which to base exact meteorological figures, but it is the longest period for which records are available from some of the stations.

When the "degrees of wetness" for each separate month are enumerated, greater disparities between the rainfall regimes of the various stations are shown, than are demonstrated by the "degree of wetness" for whole years. There are included in the table only two stations—Tamale and Salaga—which are subjected to a Sudanese (single maximum tropical) regime, without a break in the wet season; but although all the other stations have a Guinea (two maxima tropical) regime, with two distinct wet seasons, yet they differ greatly in the intensity of the main dry season, November to January.

Inspection of Table I will show the differences between the distribution of rainfall in the various localities, and will demonstrate that a station like Kintampo, which throughout the wet season has much more rain than a station like Nsawam, has yet a more intense dry season.

It is the aim of this paper to suggest that it is the rainfall of the dry season, rather than that of the whole year, which must be considered as the factor limiting the growth of the various types of vegetation, and especially that of cacao. A convenient measure of the intensity of the dry season is furnished by the "degree of wetness" for the dry months, as shown in the last column of the table.

If the stations are grouped according to the "degree of wetness" of the dry season, such grouping will correspond closely to that of the zones of vegetation; this subject is discussed in a paper, not yet published, by Mr Moor of the

Table I. *Degrees of wetness.*

Degrees of wetness

Station	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Whole year	Nov.–Feb.	Floristic zone
Tamale	0·0	0·1	4·1	3·2	7·0	6·9	8·0	12·3	14·2	6·1	0·1	0·0	42·5	0·7	Inland
Salaga	0·0	0·1	1·0	4·8	7·5	10·0	6·2	5·6	17·4	8·4	0·5	0·0	45·7	0·6	Sudanese (savannah)
Kintampo	0·0	0·3	3·8	8·2	10·5	23·1	9·6	4·5	25·2	12·6	1·4	0·0	78·2	3·8	
Kete Krachi	0·2	0·4	2·5	4·3	6·1	14·2	9·9	5·5	17·6	16·2	2·4	0·1	67·0	9·6	Transition to savannah
Wenchi	0·0	0·3	1·8	7·2	9·8	16·2	3·3	1·4	13·5	12·3	1·0	0·0	50·7	3·3	
Sunyani	0·0	0·2	3·4	5·6	5·5	8·5	3·8	0·6	16·7	16·5	0·8	0·0	43·1	1·9	
Ejura	0·0	0·4	3·2	6·3	8·6	10·3	3·0	1·0	11·7	11·8	2·9	0·0	51·2	6·6	
Kumasi	0·0	0·6	7·9	7·2	8·9	15·8	4·5	1·5	13·4	17·3	4·6	0·3	71·6	13·6	Deciduous forest
Juaso	0·0	0·9	9·0	8·2	9·4	15·6	7·5	3·3	19·4	20·5	4·8	0·6	90·0	17·0	
Wiawso	0·0	0·5	7·1	10·7	20·9	44·8	15·0	4·8	22·9	20·1	10·5	0·8	126·5	27·0	
Dunkwa	0·1	0·5	5·6	9·2	9·1	21·4	7·0	0·8	9·3	14·3	9·2	0·9	77·6	21·8	
Tarquah	0·8	2·6	6·3	6·4	15·3	35·2	4·1	2·2	8·0	19·1	13·2	2·7	111·1	60·0	Evergreen forest
Oda	0·1	1·3	7·6	7·3	9·6	13·8	2·5	1·4	8·5	10·4	9·4	2·7	70·8	36·0	
Anyinam*	0·2	3·4	9·7	10·4	14·9	17·0	8·9	3·0	17·7	24·4	8·7	1·0	87·5	35·5	
Kibi	0·2	2·4	10·6	8·9	12·0	21·8	8·1	2·1	14·3	14·3	5·0	3·0	101·6	36·6	
Koforidua	0·3	1·4	6·1	7·9	7·9	17·3	3·4	1·6	7·0	7·9	5·1	2·3	67·0	26·6	
Ho	0·4	0·6	3·9	4·1	6·9	11·9	4·4	2·8	5·8	7·4	6·5	0·7	50·0	23·9	
Kpeve†	0·2	1·1	5·2	4·5	7·4	13·0	4·3	7·0	10·1	11·6	1·6	0·7	64·4	12·6	
Aburi	0·3	0·8	4·3	3·9	6·2	15·9	4·3	2·2	6·7	8·1	4·4	2·0	59·5	21·5	Transition to savannah
Nsawam	0·2	0·4	2·2	1·5	5·1	10·7	0·9	0·5	2·9	6·5	2·7	1·4	28·1	12·4	
Asuansi	1·3	1·4	2·2	3·5	9·3	16·5	2·6	2·1	5·2	10·2	4·6	1·4	58·5	24·3	
Akuse	0·1	0·5	2·2	4·3	4·8	9·5	0·7	0·1	3·2	4·0	1·4	0·6	25·2	6·5	Coastal
Accra	0·1	0·4	1·0	1·8	6·9	7·7	0·7	0·3	1·7	2·0	0·4	1·3	19·5	8·0	Sudanese (savannah)
Saltpond‡	0·0	0·0	2·2	1·9	7·3	4·6	0·5	0·5	0·4	1·1	1·2	0·7	15·7	4·2	

* For years 1926, 1927, 1929, 1930.
† For years 1927, 1928, 1929, 1930.
‡ For years 1926, 1927, 1928, 1929.

Forestry Department, Gold Coast. But it is noteworthy that all the stations which are in important cacao-producing areas have a "degree of wetness" for the dry season of over 10 units, however low the figure for the whole year may be.

Conditions in Togoland appear to differ from those to the west of the River Volta; for from the figures of the stations there—Kete Krachi, Ho and Kpeve —it might be expected that the climate would be suitable for widespread cultivation of cacao. Yet at the present time most of Togoland is under vegetation of the savannah and savannah forest type, the cacao being in small patches on packets of good soil on the slopes of, or at the base of, the hills.

In this area the effects of the burning of bush to make clearings for farms are especially conspicuous, and it may be that this practice of burning, either for the purpose of farming or for hunting, has been followed for a longer period or more intensely than has been the case in most parts of the Gold Coast Colony. The bad effect of shifting cultivation may be seen in parts of the colony which have a climate like that of Togoland, and it is probable that the present condition of Togoland represents an advanced stage in this degeneration. This theory is supported by the fact that in the thinly populated area between the Rivers Menn and Wawa in the Ho District in Togoland, there still survives a large stretch of deciduous forest.

Mention has been made elsewhere (7, 8) of the importance of edaphic factors in areas where the climate approaches the limits of desiccation which can be withstood by cacao, and Togoland exhibits many striking examples of this fact. For instance, Ho appears to have a climate more suitable to the growth of cacao than that of Kpeve; yet near Ho there are only a few small patches of cacao in sheltered positions; while at Kpeve there is an excellent plantation of cacao growing in a patch of deep loam, and watered by seepage from the hills above.

At Asuansi, where rainfall is fairly evenly distributed throughout the year, the type of vegetation probably is influenced by the very sandy nature of the soil.

The influence of the dry season on the cultivation of cacao.

Not only does it appear that a very marked dry season will inhibit the cultivation of cacao, but also that when the cacao does survive a less intense period of drought, it may be profoundly influenced. This influence of the dry season has an important bearing on many aspects of the growth and cultivation of cacao:

(1) *Fruiting*.

Figures from the experiment stations of the Department of Agriculture (9) demonstrate that on stations having a well-marked dry season, the main crop of cacao is later than in those districts which are subject to less variation in rainfall.

(2) *Vegetative growth.*

Even more important is the influence of the dry season on the vegetative growth of the trees. It is probable that constant regular growth is not a quality inherent in the cacao tree—in the more equable climate of Trinidad there are well-marked flushes of new leaves—but it is certain that the "deciduous habit," often seen in the Gold Coast, is quite abnormal.

There are available no observations to show to what degree this leaf fall is due to the influence of the actual harmattan—the hot dry wind—and to what degree it is caused by the cumulative effect of the dry season on the humidity of the air and of the soil. But it is probable that the latter is the more important factor, for the leaf fall may be observed in dry seasons when the harmattan has scarcely been felt in the cacao-growing areas.

(3) Sahlbergella *attack.*

Sahlbergella spp., sucking insects which attack the young twigs, are the most important pests of cacao in the Gold Coast, and their control is a major problem in the country. Where there is a severe dry season, producing a check in the growth of cacao, and a subsequent marked flush of new leaves and new twigs, the damage caused by the insects is enhanced; if the rate of growth were less variable, the damage would be minimised.

For other crops, the water balance of the plants is a very important factor in their resistance to insect pests (**10**); therefore it would be interesting to see whether the *Sahlbergella* problem might not be solved, in some cases, by the irrigation of the cacao farms once or twice during the dry season. There would be many practical difficulties, especially in the present time of depression; but in the Bisa area, which includes some of the best cacao-growing soil in the country, and where, in spite of a dry climate, a great deal of cacao is grown in narrow river valleys, irrigation on a small scale might be feasible.

(4) *Soil cultivation.*

Few cacao farms in the Gold Coast have received any soil cultivation, the growth of weeds being checked by cutlassing: in consequence the majority of the feeding roots of the cacao appear to be within a few inches of the surface. If cultivation were commenced on an established farm, it would therefore be safer to do so during the months of April to August; for if deep cultivation were made during the dry season, or just before it, the trees would receive a violent, or even a fatal, check.

(5) *Manuring.*

The trials of the Department of Agriculture (**11**) have shown a comparatively small response of cacao to manurial treatment. It is possible that as the stations (Kpeve, Kumasi, Asuansi, and Aburi) at which these trials are prosecuted are all in the drier cacao-producing areas, there are involved climatic

limiting factors, and that trials in wetter localities would yield more definite conclusions.

The results of these trials are expressed as yields of cacao, but it is probable that the manures have also influenced the vegetative growth of the trees—a most important factor; for any treatment which will prolong the life of a cacao tree under dry conditions will be of great value in the Gold Coast.

Further, the response of the trees may be controlled by the season of the year at which the manure is applied, as is the case in the treatment of temperate orchard crops.

Therefore it would appear that cultural operations, which are practised in cacao-producing countries that enjoy a well-distributed rainfall, might be applicable to those parts of the Central and Western Provinces which are not subject to prolonged drought at any time of the year; yet these operations might need considerable modification before they were employed in those areas which have a strongly marked dry season. And it is in localities which have a distinct dry season—the Eastern Province and Ashanti—that the bulk of the Gold Coast cacao is grown.

The annual incidence of a period of drought has also an important bearing on the types of cacao trees which are required.

In the Gold Coast the yields of cacao are often very high, but the life of the tree is often very short; the relatively dry conditions of the country may be instrumental in both these phenomena, which are comparable to the effects produced when apples are grown on shallow-rooted dwarfing stocks (**12**).

Preliminary investigations (unpublished) by the author in Trinidad showed that there were significant differences between the progenies of various trees with regard to the root/shoot ratio. It should be possible to isolate types of cacao with well-developed root systems, more resistant to drought, and longer lived, which would be of great value in the Gold Coast.

SUMMARY.

1. It is suggested that, in the consideration of rainfall as a factor limiting the cultivation of cacao in the Gold Coast, regard should be paid to the degree of wetness of the dry months (November to February) rather than to that of the whole year.

2. The intensity of the dry season has a very important bearing on most aspects of cacao cultivation and selection.

REFERENCES.

(1) **Myers, J. G.** "Notes on wild cacao in Surinam and in British Guinea." *Bulletin of Misc. Information* (Kew). No. **1**, pp. 1–10, 1930.

(2) **Chipp, T. F.** *The Forest Officer's Handbook of the Gold Coast, Ashanti and the Northern Territories,* pp. 34–46.

(3) **Chipp, T. F.** *The Gold Coast Forest; a study in Synecology,* pp. 22–37.

(4) **Auchinleck, G. G.** "Rainfall of the Gold Coast." *Bulletin No.* **2** *of the Department of Agriculture, Gold Coast,* pp. 8–10.

(5) **Chamney, N. P.** "The climatology of the Gold Coast." *Bulletin No.* **15** *of the Department of Agriculture, Gold Coast,* pp. 8–10, 21–2.

(6) **Adams, J. M.** "Meteorological Records in the Gold Coast for 1929." *Department of Agriculture Year Book,* p. 366, 1929.

(7) **Muir, J. C.** "Survey of cacao areas—Western Province, Ashanti." *Department of Agriculture Year Book,* p. 58, 1929.

(8) **Thomas, A. S.** "A note on the deterioration of cacao in the Bisa area." *Department of Agriculture Year Book,* pp. 95–8, 1929.

(9) **Auchinleck, G. G.** and **Knowles, C. H.** "Yields of cacao on experiment stations." *Bulletin No.* **4** *of the Department of Agriculture, Gold Coast,* p. 10.

(10) **Mumford, E. P.** and **Hey, D. H.** "The water balance of plants as a factor in their r - sistance to insect pests." *Nature,* 3150, **125**, 411–12.

(11) **Beckett, W. H.** "Results of Cacao Manurial Trials." *Department of Agriculture Year Book,* pp. 99–111, 1929.

(12) **Hatton, R. G.** "Apple root-stocks, their particular suitabilities for different soils, varieties, and purposes." *East Malling Research Station Ann. Rept.* pp. 46–52, 1925.

THE PRESENT VEGETATION OF ARTHUR'S PASS (NEW ZEALAND) AS COMPARED WITH THAT OF THIRTY-FOUR YEARS AGO

By L. COCKAYNE,

Hon. Botanist, State Forest Service, N.Z.

AND J. W. CALDER,

Lecturer in Botany, Canterbury Agricultural College, N.Z.

(*With Plates XVIII–XX and one Figure in the Text.*)

I. INTRODUCTION.

ARTHUR'S PASS is a rather narrow saddle at an altitude of 930 m., situated in the Southern Alps between the lofty masses of Mt Rolleston (2257 m.) and Temple Peak (2000 m.) at about latitude 43° S. The pass is bisected by the high road which leads from the Canterbury Plain to the west coast and passes through the famous Otira Gorge, so that its beautiful expanse of wild flowers is well known to the general public. From the standpoint of our paper, this road is of particular importance as forming a definite starting-point for dividing the plant covering of the pass into distinct sections; while the road itself forms a new edaphic habitat for plant colonisation.

In the early nineties of last century a considerable part of the vegetation was burned by those engaged in making the survey for the Midland Railway. Thanks to the nature of the plant life and to the extremely wet climate the ground, laid bare by the fire, became rather rapidly reclothed with plants, so that by the summer of 1897–8 there were many new successions, some of which might easily have been mistaken for primeval. There were also many unburnt patches so that it was possible to compare with fair accuracy the floristic composition of the original and the new communities. Camping on the pass during most of December, 1897, and January, 1898, L. Cockayne was enabled to study the original communities and the new successions, with the result that he published a paper on the subject (1899, pp. 398–419) which was probably the first of its kind in the British Empire, and perhaps the first anywhere subsequent to the incoming of botanical ecology. More important still is the fact that he took a good many photographs, showing both the progression of events and examples of unburnt communities. We have been able to locate the exact points from which these photos were taken, so that we have the good fortune, by means of photography, to exhibit side by side in our pictures examples of successions as they were in 1897–8 and as they now are—34 years later. Also, with the above fairly detailed account of the

former vegetation in our hands, we have been able to ascertain, in the field, the present position of affairs as compared with that of 1897–8, and to gain some idea how the change has come about. Both of us, working together, took notes of certain of the new successions in May, 1930, but these have been extensively supplemented by Calder during several subsequent visits. The latter investigator has also established permanent quadrats, etc., so that the progress of events may be followed for a good many years to come, and actual competition can be studied intensively. It is intended that an account of the gradual changes which are proceeding will form the subject of future papers. Nor need this particular line of investigation cease with the labours of Calder, but the future papers and notes should supply such definite information as will allow others to carry on this work. The site, situated as it is in a carefully guarded National Park, offers an ideal chance for that much-needed ecological study—the vegetation changes, slow or rapid—which take place during a considerable period. The time, however, appears ripe for a brief account of some of the most important changes, etc., which have taken place since Cockayne's early, tentative study of 1897–8. It will also serve to give a broad view of the leading types of vegetation from which future comparisons may be made.

Before concluding these introductory remarks we must express our great indebtedness, first of all, to the Arthur's Pass National Park Board in furthering our aims, and in the next place to the New Zealand Institute for allotting the junior author a substantial research grant which is enabling him to carry out the preliminary investigations, on which basis his further work will be undertaken.

II. BASIS OF COCKAYNE'S 1899 PAPER.

(a) The primitive vegetation.

The mountains in the neighbourhood of Arthur's Pass form the northern limit for true glaciers in the South Island. The pass itself, the mountain slopes and the heads of the two main rivers (Bealey and Otira) show everywhere strong signs of glacial action, especially in the morainic deposits—these rendering the surface of the pass most irregular and in some places extremely rocky. It cannot have been long, geologically, since the pass was covered with ice, because not only are there small glaciers at no great height therefrom, but considerable snow fields—glacier-like in character—lie at the heads of both the Bealey and Otira. The vegetation at the time the pass was discovered (1864) would be purely primitive and would resemble, to no small degree, that now found in the cirques of the eastern glacial New Zealand rivers, near the terminal faces of those larger valley glaciers which flow into them. Briefly, this primitive vegetation falls into subalpine scrub and L. Cockayne's class, "Herb field," which he defines as follows (1928, p. 310): "Herb field is distinguished by the abundance of various large herbs—some more or less meso-

phytic—which may either dominate, or tall tussock grasses or even shrubs may be the dominant life form. The vegetation is generally closed, but open herb field must also be distinguished where the composition is virtually that of closed herb field." He subdivides the formation into three classes: (1) herb field proper, (2) shrub herb field, and (3) tall tussock herb field. The last two alone would be represented in the primitive vegetation we are now discussing. Indeed, as will be seen further on, it seems probable that herb field proper was very rare or perhaps altogether absent in primitive New Zealand. There would also be, as now, more or less bog vegetation with Sphagnum dominant. The virgin vegetation may even from time to time have been destroyed in places by natural fire—the result of lightning—but such is just as much a natural factor as are the more commonly recognised ecological factors—heat, light, wind, etc.

(b) *The burnt vegetation and its subdivisions.*

As a rule, when the settler comes in contact with the natural vegetation of any area, he soon sets it alight—frequently for economic reasons, but not seldom through leaving unextinguished the fire on which he has prepared his food, or else burning merely for the sake of seeing a blaze. In short, vast areas of vegetation have been destroyed by fire in New Zealand, purposely or accidentally. The West Coast road was traversed during the sixties of last century by thousands of gold diggers, and it is most unlikely that the easily burnt shrubs on either side of the road can altogether have escaped destruction. During the survey for the Midland Railway in 1890, the greater part of the vegetation of Arthur's Pass was deliberately burned, so that burnt and unburnt portions stood out clearly in 1897. Cockayne also states that there was an earlier fire for which he could give no exact date, but his estimate was that it occurred at the end of the sixties.

In order to draw comparative conclusions, L. Cockayne divided the vegetation of the pass into seven sections named respectively A, B, C, D, etc., each section being designed to show the effect of fire on different classes of vegetation; e.g. *Nothofagus* forest, scrub forest, subalpine scrub and shrub herb field—to mention the principal communities. For each of these classes details are given regarding the unburnt portion and the new succession, in some cases the number and size of the individuals on a definite area are indicated. These sections range from the Otira Gorge near Peg Leg Creek to the *Nothofagus* forest at the southern end of the pass, and from the base of Temple Peak to the base of Mt Rolleston spur. In addition to the details given in Cockayne's paper, photographs were taken by that author of certain areas which were presumably primitive but which were excluded from the burnt section. These areas we have located, so that *we are in a position to deal with the ordinary progression of events in a closed virgin vegetation during 34 years—a fundamental matter on which plant ecology is usually silent.*

III. THE FLORA OF ARTHUR'S PASS.

By Arthur's Pass we mean the whole of the saddle lying between the two ranges, together with the flat ground from Peg Leg Creek to the base of the great western mass of stony débris over which the West Coast road ascends before it descends into the Otira Gorge.

The flora consists of 274 species together with certain well-marked varieties and hybrid-groups, many of the latter forming large swarms in nature. The species and hybrids fall into 47 families and 114 genera of which the largest are: (families) Compositae 53, Gramineae 31, Cyperaceae 18, Scrophulariaceae 17, Rubiaceae 15, Umbelliferae and Epacridaceae 11 each; (genera) *Celmisia* 18, *Coprosma* 13, *Olearia* 10, *Danthonia* 8, *Senecio* 7, *Poa, Anisotome* and *Dracophyllum* 6 each.

Of more importance, ecologically, than the species are the life forms, and these may be grouped into the following general classes, to each of which is appended the number of species which it contains: trees 12, shrubs 55, semi-woody plants 54, herbs 80, grass-like plants 44, ferns 11, rushes 8, water plants 5, parasites 3, epiphytes 2, spot-bound plants 150, creeping plants 124. Really these figures are somewhat misleading, for a number of species occur on a substratum which was hardly, if at all, affected by fires; in fact, the life forms of real moment are the trees, the shrubs, the tussock grasses, and the larger herbaceous and semi-woody plants. Had the flora, not only of the pass, but of the adjacent mountains been considered, the totals would have been much higher.

IV. THE ECOLOGICAL CONDITIONS.

So far as instrumental weather records for the pass itself are concerned, except for a few taken by Cockayne in 1897–8, none are available. It might seem by this that we possess nothing of importance regarding the weather conditions to which the plants are exposed, yet, were lengthy records available, as taken by the ordinary means, they would tell us but little regarding the relation of plants and weather; while some general statement may afford an overseas botanist some idea of the conditions which the life forms of the species have to meet. Taking such life forms, rigid stems, thick leaves, and a close habit of growth—sometimes extremely dense—are frequent among the shrubs; while though there are certain large-leaved herbaceous plants such leaves are usually deciduous, and in a majority of cases the herbs and semi-woody plants are of low growth, their leaves small and their stature from quite low to actually hugging the ground. In fact, the vegetation as a whole has a sub-xerophytic facies. We have brought this position of affairs to the fore, because it might well be thought rather curious in a climate so wet as that to be described. In fact, the rainfall, judging from the records at the two nearest meteorological stations—Otira (average yearly rainfall during the

last 25 years, 1905–30: 5025 mm.) and Arthur's Pass township (average yearly rainfall, 1914–30: 4000 mm.)—is probably considerably higher than at either station and the number of rainy days greater (Otira, average number of wet days, 1905–30: 161; Arthur's Pass, average number of wet days, 1914–30: 146).

As for the climate as a whole, we present an account published by Cockayne (1900, pp. 131–2) based on his experience and notes taken during the time he was studying the vegetation of our area in the summer of 1897–8—a period which we think may be taken as a fair average. This is what he says: "during that time it rained on more than half the days, the rain sometimes lasting for two days and a half at a time. There was one heavy thunderstorm. My tent, situated on a usually quite dry spot, was not infrequently filled with water to a depth of 15 cm. The wind blew north-west during the whole of the six weeks, with the exception of a few hours, when a south-west wind gave a slight sprinkle of snow. Once, too, it snowed from the north-west. The wind blew often with enormous force. Had our tents not been sheltered by the trees they would have been frequently levelled to the ground. This excessive wind has written its mark on the vegetation, e.g. the tussocks of *Danthonia Raoulii* are all bent to the South-west. Often, when not raining on the pass, it was doing so on the adjacent heights, and when raining on the pass was fine in the Otira Gorge (W.). During the fine weather it was extremely hot, so much so as to make climbing an exertion. For a few days before our arrival it had been fine, and then the ground and all the vegetation was so dry that one had to be most careful when lighting a fire not to set the forest in a blaze. A small creek near the camp was perfectly dry, and so were many water-courses; yet the rain previous to these few fine days had been excessive for weeks." Again, on p. 133 (*loc. cit.*): "In December, 1898, while on an excursion with Prof. K. Goebel, we had an opportunity of observing the vegetation of this region under conditions of dryness, for during the fortnight we were in Westland only a few local showers occurred....So dry was the subalpine scrub on Arthur's Pass that some of a party with whom we were camped, climbing Mt Rolleston, set fire to a considerable portion. Much of the usually swampy ground was quite dry and the plants which generally were surrounded with water were growing on extremely dry ground. Outwardly, except as shown by the presence of certain hygrophytes, there appeared nothing to indicate the extremely moist climate." Under exceptional circumstances there may be much longer periods of dryness than mentioned above, so that there can be little surprise at the sub-xerophytic facies of the vegetation as a whole or the truly xerophytic structure of many of its members. A plant, in order to cope with a variety of conditions of rainfall, must be attuned to the minima and not to the maxima or it will go to the wall, but in the case of temperature and wind the contrary stands. We have already mentioned the violent wind, and the effect of this factor upon the distribution, height and density of the vegetation exposed thereto can hardly be overestimated. Hemmed in between

lofty mountain walls the north-west wind blows with the utmost violence and, unless accompanied with rain, transpiration must reach a degree most unexpected in so wet a climate. Naturally, as the plant covering of bare ground turns into thickets of rigid thick-leaved shrubs, there is abundant room within this new community where even hygrophytes can become established. The snow factor differs considerably from year to year. Some years snow may lie on the pass only for a week or two at a time, or even less, and during other years many of the plants may be buried for several weeks with a snow covering of 60 cm. or even far more. Frosts occur during each month of the year, but we hold the opinion—judging from the behaviour of New Zealand high-mountain plants in Britain and the Continent of Europe—that the winter cold seldom exceeds $-16°$ C. and that $-12°$ C. may be a fair average (1925, pp. 75–80). In the case of frost, too, it makes all the difference whether a plant is in a position to be covered with snow or for that to be impossible. The mechanical effect of snow, as will be seen further on, is a point not to be neglected. The edaphic habitat, i.e. the soil in its widest sense, varies greatly on different parts of Arthur's Pass and ranges from that of extremely stony moraine to that where water lies all the year round. Obviously a soil exposed to so much heavy rain and clad with a closed plant covering for so long a period must be strongly peaty, but the subsoil to a greater or less depth is a boulder clay. Of course where a fire has raged and the vegetation was shrubby a large part of the humus will be burned, and soil conditions be established distinct from those of the present time, but approximating to those which existed near the receding ice at the close of the glacial period. In such new ground there will be no seeds, so that there is an equal chance for the present-day exotic and the ancient New Zealander to come into competition. What happens in this regard is detailed further on.

V. Some outstanding features of the new vegetation together with references to the conclusions in the 1899 paper, and certain matters connected with the species.

At the present time the Arthur's Pass area—river bed, some bogs, streams and tarns excepted—is clad with a fairly continuous plant covering and the bare ground and the embryonic communities of 1897–8 have passed away. The vegetation itself is far from homogeneous and from its diversity can be learnt the lesson of the relation of the diverse communities to the diverse edaphic habitats. With the account of the vegetation as it was in 1897–8 in our hands, we have been able to form some idea, if not of the entire progression of events, at any rate of some of the changes which have come about, and in certain cases we can with confidence give the reasons for such changes. Furthermore, in the paper of 1899 the author—perhaps overbold for those days when the idea of succession had hardly been mooted—drew certain conclusions as to what had happened and would possibly take place in the future,

and of course the first question was to ascertain—a quite easy matter—how far these conclusions were justified. In what follows these conclusions form part of our text, but other matters which seem to us of special ecological importance are dealt with more fully. Here for the sake of clarity we present our results each under a separate number.

(1) *Successions in general after burning shrubland or shrub herb field.* A study of the various successions here indicated is not only of scientific moment, but it should have an important bearing on the treatment of those splendid heritages of the nation—its great National Mountain Parks (The Tongariro, The Egmont, The Arthur's Pass, The Mount Cook, and The Fiord) for in parts of them at least, it seems feasible to bring into being areas of herb field proper with its wealth of fine flowers.

It has already been shown (Cockayne, 1899, pp. 389–419) that where the subalpine scrub and shrub herb field had been entirely burned the first succession consisted of an assemblage of various species of herbs and semi-woody plants, amongst which were conspicuous the tall erect rosettes of *Celmisia coriacea* and its allies, the broad colonies of *Ranunculus Lyallii*, the equally beautiful *Ourisia macrocarpa* var. *calycina* together with most of the herbaceous and semi-woody plants of Arthur's Pass. Where the ground was particularly stony this early stage of succession persisted for many years, and in some places is as yet more or less in evidence. Even on wet ground where the substratum is more or less hostile to herb field proper the first succession consisted largely of this community but with *Celmisia petiolata* dominant rather than *C. coriacea* (Pl. XX, phot. 5). At the present time in other places there is shrubland, but by no means the same as that of the original vegetation. For example, the south face of the moraine above Lake Misery was clothed with subalpine scrub consisting of *Dracophyllum longifolium*, and *Phyllocladus alpinus* as the dominant elements (1899, p. 408). The new plant covering in 1897–8, seven years after the fire, was scanty and consisted of young plants of *Hebe canterburiensis* in large quantity, *Coprosma serrulata*, *Senecio elaeagnifolius*, *Cassinia Vauvilliersii* and *Dracophyllum longifolium*. The present plant covering of the moraine is a dense scrub 1 to 2 m. high with *Dracophyllum longifolium* and *Senecio elaeagnifolius* dominant. The story of succession can be read at the present time on an area which has been studied by Cockayne and Sledge to the south of the pass. An area of shrub herb field which was burnt about a year ago is also under observation and permanent quadrats have been located on it.

(2) *Podocarpus scrub replaced by shrub-composite scrub.* In the original burn a considerable piece of subalpine scrub with a south-westerly aspect was burned. This fronted a portion of the *Nothofagus* forest that abuts on the pass at its lower end. This scrub, a part of section C according to the original notes, was strongly dominated by the tall shrub or small tree, *Phyllocladus alpinus*, for apparently about three-quarters of its tall members were that

Photo. L. Cockayne, January 1898.

Phot. 1. Condition of the burnt *Phyllocladus* scrub as in January 1898; *Nothofagus* forest in the centre.

Photo. J. W. Calder, January 1931.

Phot. 2. The same area as shown in Phot. 1, but now the vegetation is Shrub-Composite scrub.

COCKAYNE—THE PRESENT VEGETATION OF ARTHUR'S PASS AS COMPARED WITH THAT OF THIRTY-FOUR YEARS AGO

conspicuous species. A photograph taken in January, 1898 (Pl. XVIII, phot. 1) shows mainly a mass of burnt shrubs, hardly any of the small new invaders being visible. In 1897–8 the most striking feature of the new growth was the deciduous, far-creeping fern, *Hypolepis millefolium*, 30 cm. high, its presence doubtless due to the abundant light. At the present time this plant has disappeared as was expected, except in open spaces where it forms patches in the herb field proper. Another abundant plant was the small *Hebe canterburiensis* which, it was anticipated, would "most likely in time form the greater part" of the new community; but the expectation fails, for at the present time it is so rare as to have escaped mention in our first notes. The outstanding feature of the new scrub now 2 m. high or more and extremely dense, is that *Phyllocladus alpinus* is no longer dominant, its place having been taken by *Senecio elaeagnifolius*, a composite shrub with an extremely different life form, and this is associated with its ecological and taxonomic allies *Olearia ilicifolia, O. lacunosa, O. arborescens* and hybrids in which these three are concerned. Apparently, too, *Coprosma pseudocuneata* is far more common than in the original scrub (Pl. XVIII, phot. 2). Permanent quadrats have been marked off in this scrub, and in connection with these a detailed account of this interesting new community will be prepared in due course. Among the early comers was a good deal of *Phormium Colensoi* and this in many places is still abundant, but where the scrub is densest it has been suppressed.

(3) *Succession in a dying* Nothofagus *forest.* Cockayne's camp in 1897–8 stood on the outskirts of the great forest mass which dominates all the eastern slopes of those mountains enclosing the Bealey Valley. At that time, so far as memory serves, there were few, if any, dying trees. During the period which has elapsed since 1897 in one part of the forest a large proportion of the tall *Nothofagus cliffortioides* has died (Pl. XIX, phot. 3). There has been no regeneration of the *Nothofagus*, so that the ground is now covered with a dense growth of certain shrubs (*Coprosma pseudocuneata, C. ciliata, C. parviflora, Aristotelia fruticosa* and *Phyllocladus alpinus*) up to 4·5 m. high. These same shrubs doubtless formed the greater part of the original forest undergrowth, and to their cutting off the light from the forest floor the absence of young *Nothofagus* trees must be attributed. In an adjacent part of the forest the *Nothofagus* trees were much closer together so undergrowth such as that just described was absent, and as the trees died and more light gained the forest floor, abundant *Nothofagus* seedlings appeared, so that there is now a dense growth of saplings.

(4) *A general comparison of the shrubby vegetation at the opposite ends of the pass proper.* There was a remarkable difference between the vegetation at the northern and southern ends of the pass which can be referred with some degree of confidence to the effect of the cold snow-bringing south-west wind, as shown both by the differences in the luxuriance of growth, and by this

wind's hostility to the incoming of certain species, especially *Dracophyllum Traversii*. In the new vegetation such differences stand out with some clearness. Thus, at the northern end of the pass, on the moraine at the back of Lake Misery, the dominants are *Senecio elaeagnifolius* and *Dracophyllum longifolium*, and subdominant, or common, are *Olearia ilicifolia*, *Hymenanthera alpina*, *Phyllocladus alpinus* and diverse members of the hybrid group—*Senecio Bidwillii* var. *viridis* × *S. elaeagnifolius*. In 1897–8 the pioneer plants belonged to species other than the above, especially *Hebe subalpina*—dominant—(now rare) and a small amount of *Olearia ilicifolia*. The now dominant *Senecio elaeagnifolius* was only sparsely represented and it was here that the seedlings of *Phyllocladus* "were among the very few seen during the taking of these notes" (1899, p. 409). In the original scrub, a considerable portion of which still exists (Pl. XIX, phot. 4), the dominants were *Dracophyllum longifolium*, *Phyllocladus alpinus*, *Coprosma parviflora* and *Olearia ilicifolia*, while *Dracophyllum Traversii*, of tuft tree form, though its striking physiognomy leads to the erroneous appearance of dominance, was conspicuous in the tallest scrub, but apparently rare in the low scrub. There are a few young plants of *D. Traversii* 30 to 40 cm. high, mainly in one spot, in the new vegetation.

At the southern end of the pass there is a community with *Cassinia Vauvilliersii* and *Hebe subalpina* dominant, but in time these may be more or less replaced by *Senecio elaeagnifolius* and *Dracophyllum longifolium*, while in places *Olearia nummularifolia* is common enough, but even with the anticipated additions the species will be far less in number than at the northern end. The original unburnt scrub of this section possesses as dominants *Phyllocladus* and *Dracophyllum longifolium* with a small amount of *Hoheria glabrata*: *Dracophyllum Traversii* was entirely absent.

(5) *Tall tussock grassland versus wet herb field.* A photograph taken in January, 1898 (Pl. XX, phot. 5) shows most clearly an area of wet herb field which might well be primitive, but this cannot be so, because it could not have escaped the 1890 fire which swept the pass as a whole, though doubtless the wet nature of the ground made possible the rejuvenation of certain species of *Celmisia* and various other herbs and semi-woody plants. Where the ground was steeper and more stony, the effect of the fire was plainly visible and of course the new community, though of a herb-field character, was absolutely distinct from that of the wet ground. Pl. XX, phot. 6 when compared with phot. 5 shows the surprising change which has taken place in the wet herb field during 33 years. The great tussocks of the two varieties of *Danthonia Raoulii* and their many hybrids completely dominate the scene, so that at first we could hardly believe that an alteration so great could have occurred. It was far from easy to locate the exact point at which the original photograph was taken, but this we did, so that Pl. XX, phots. 5 and 6 show accurately the great physiognomic change which has taken place. To be sure, the re-

Photo. J. W. Calder, January 1931.

Phot. 3. Regeneration of *Nothofagus cliffortioides* forest where the trees had died naturally, showing a close undergrowth of species of *Coprosma*, etc., but no juvenile *Nothofagus*.

Photo. J. W. Calder, January 1931.

Phot. 4. Portion of original scrub near Lake Misery, showing in the background *Dracophyllum Traversii* of tuft tree form.

Photo, L. Cockayne, January 1898.

Phot. 5. Wet herb field as in 1898, occurring as an early stage of succession after the burning of the original vegetation.

Photo, J. W. Calder, January 1931.

Phot. 6. In the course of 33 years the wet herb field shown in Phot. 5 has changed into tall tussock-grassland.

placement of wet herb field by tall tussocks is not complete, for a close examination revealed the fact that many of the herbaceous plants still exist, especially *Celmisia petiolata*. With the tall tussocks are many rush-like tussocks of *Schoenus pauciflorus*, a species characteristic of certain classes of bog, especially in the eastern part of the Southern Alps which possess a tussock grassland climate. Where the soil is drier and more stony, *Celmisia coriacea* is the dominant herb. These *Celmisias* of erect rosette form are rarely killed outright by fire, since the main bud is surrounded by a close sheath of rotting leaf bases saturated with water, and so is perfectly protected from fire. To this fact is due the early appearance of great colonies of *Celmisia* wherever fire has occurred, and where they are accompanied by *Ranunculus Lyallii* it is because this species can also withstand burning, thanks to its massive, broad, fleshy rhizome. We may point out that on mountain sheep pastures where the climate is dry *C. spectabilis* has become a bad weed.

(6) *The disappearance of dominant* Gleichenia alpina *on Sphagnum bog*. It is now a well-known fact that in many cases Sphagnum bog is merely an early stage in the development of both low and tall tussock grassland; but this is most marked when the climate is fairly dry. On the west side of the West Coast road, in proceeding from the forest to the first creek, there was, in 1897 and for some years later, a good deal of Sphagnum bog with abundant colonies of the wiry *Gleichenia alpina* growing upon the Sphagnum cushions. At the present time this fern is absent and the area now contains a vegetation consisting of tall tussock grassland with *Hebe buxifolia* var. *paucibrachiata* growing amongst the tussocks. On one point on the left-hand side of the West Coast road between the Arthur's Pass township and the pass, after crossing McGrath's Creek, there was a considerable area of Sphagnum bog with many bushes of the usual species of *Dacrydium*, various species of *Celmisia*, *Astelia Cockaynei* and probably *Gleichenia alpina*. This bog was burned some years ago and it is now mostly tall tussock grassland.

(7) *The persistence of* Ranunculus Lyallii. The following is the description of *Ranunculus Lyallii* given by Cockayne (1928, p. 239): "The famous mountain lily...is confined to the South Island and is common on wet mountains from the south of the Spencer Mountains to Stewart Island. The Western District is its headquarters. It forms colonies many square metres in extent, to the almost complete exclusion of all other plants. Each individual consists of a large, fleshy, broad, thick rhizome furnished with abundant, descending, stout, flexible roots. As the plant grows one end of the rhizome decays while the apex increases in length, the plant thus occupying new ground. From the apical end of the rhizome, long petioled, peltate leaves are given off, the petioles vertical and the blades horizontal, thus effectively shading the ground beneath. The leaf blades are smooth, bright green, flexible, coriaceous and frequently form a saucer-like surface which is filled with water after rain. The petioles are stout, they measure 30 cm. or more in length, and the blade

may be 24 cm. or more in diameter. The flowers, borne on tall branched stalks rise high above the foliage. They are pure white, the petals at times so numerous that the flower looks semi-double, and thirty blossoms to a stalk, each 7 cm. in diameter are quite usual. It may easily be seen, then, what a glorious spectacle is a hillside clothed as far as the eye can see with close colonies of this noble plant. Nor is it when it is in bloom alone that it is striking, for, when not in flower the great leaves, almost knee deep show more plainly their unusual form." From the above description it can clearly be seen that the life form of this plant is strongly hostile to the incoming of other species on the ground it occupies. The long persistence of colonies of this plant is supported by the fact that photographs of a colony by Cockayne in 1898 and Calder in 1931 show comparatively little change, and the colony may remain inviolate for many years to come. Even the aggressive semi-tree fern *Polystichum vestitum* is suppressed, and the still more aggressive *Danthonia Raoulii* var. *rubra* has advanced little, if at all.

(8) *The disadvantage of possessing a certain life form.* In section C of Cockayne's early paper there are now a considerable number of the erect *Hebe buxifolia* var. *paucibrachiata*, though the above author did not mention such in his original notes. These are doomed to extinction on account of their life form, which one would never suspect of being disadvantageous. The following is based on our notes taken on the spot. *Hebe buxifolia* var. *paucibrachiata* is an evergreen shrub made up of numerous, erect, sparingly branched stems which arise from a small base. In the new growth of section C already described this life form is altogether changed, the stems now extending upwards and outwards, thus taking on a goblet-like form at the bottom of which are now growing, as in a flower pot, the following species: *Ranunculus Lyallii, Aristotelia fruticosa, Nothopanax Colensoi, Astelia Cockaynei, Phormium Colensoi* and *Phyllocladus alpinus*. The tall *Hebe* becomes straggly, and when the big bushes reach about 2 m. in height they are weighed down during snow falls and do not recover when the snow melts, because of the weight of their shoots and the length of their stems. From this goblet-like opening a new minor succession arises, the *Hebe* being wiped out.

(9) *The conclusion that* Hebe *was predominating and would possibly predominate.* Taking the conclusions, some of them more or less prophetic (Cockayne, 1899, pp. 416–18), which were based on the early study of the new vegetation in 1897–8, all of them, except two, are shown to be true, or nearly so, by a study of the vegetation as it now is. That "prophecy"which relates to the early establishment of herb field, may, we think, be looked upon as a general ecological law for all parts of the New Zealand region where high mountain plants can establish themselves. Also we would add another law, viz. that tall tussock grassland is extremely powerful in suppressing fell field, herb field and bog. The prophecies which apparently do not hold good are those suggesting the dominance of *Hebe* (shrubby veronicas). Such dominance

would assuredly have occurred in many places, and for a time *Hebe subalpina* was a distinct dominant. At the present time this species is much less in evidence owing to the fact that for some unknown reason example after example has died; the cause perhaps being the attack of some fungus or virus disease. It may be, too, that advancing age has something to do with the matter, for in the course of time many forms of *Hebe*—as already shown— become straggly and unsuited to combat high winds or heavy snow.

Fig. 1   Low scrub of *Dacrydium Bidwillii* photographed in May 1930, but almost exactly as it was in December 1897.

(10) *The present state of an unburnt piece of scrub belonging to a subassociation undescribed in "The Vegetation of New Zealand."* The scrub in question (Fig. 1) grows on the wet peaty ground between Lake Misery and the base of the moraine, occupying a flat surface, and the combination has not been recorded for any other part of the New Zealand region. It consists of *Dacrydium Bidwillii* together with more or less of the following: *Hebe buxifolia* var. *paucibrachiata* and *Coprosma propinqua*, while on the drier ground is a certain amount of *Hymenanthera alpina* and tussocks of *Danthonia Raoulii* var. *rubra*. On the floor is a dense carpet of *Dacrydium laxifolium* with here and there *Coprosma ramulosa*. The scrub ranges from about 60 cm. to 90 cm. high. The chief point of interest of this scrub in regard to this paper is that it is almost

exactly as it was 33 years ago in height and structure (1899, p. 409), although *D. Bidwillii* is occasionally a small tree elsewhere. The scrub might well have been expected to increase in height but apparently it had reached its maximum long before the fire occurred. Its density, too, forbade any other plant to enter in. During February, 1931, and again in April, following rainy periods, the lake rose and covered the greater part of this community to a depth of 10–50 cm. for more than a week, but this water drained away very rapidly when the rain ceased, and such submersion if frequent might account for this suppressed growth of the scrub.

(11) *Exotic plants in the new vegetation.* Within a distance of about 5 km. southwards from the highest point of the road over the pass, there are at least fifty species of naturalised foreign plants, many belonging to the class known as weeds, i.e. they are, in general, species of easy distribution, their seeds being highly viable. The headquarters of these invaders is the roadside, the river bed of the Bealey, and the waste ground near the Arthur's Pass township. There are also a good many on the roadside up to the head of the Otira Gorge; others again occur on the flat low-lying ground near the centre of the pass, which for many years was the camping ground for sheep and cattle driven over the pass. The north-easterly and south-westerly gales should be most active in carrying the seeds of exotics into the vegetation of Arthur's Pass generally, and one might well expect that on the bare ground after a fire many exotics would settle down. At the time of Cockayne's early examination the following species were reported as occurring, but in small quantities, close to the road in section A: *Stellaria media, Holcus lanatus, Trifolium repens, T. pratense* and *Rumex Acetosella.* At the present time, excluding the recently burnt areas on the pass, the roadside and also the large grassy area which was used as a stock camp for many years, there appear to be virtually no exotics present, for evidently such cannot survive in competition with the indigenous plants. In an area burnt in 1930, the following exotics were noted: *Cerastium vulgatum, Hypochaeris radicata, Rumex Acetosella, Holcus lanatus* and *Agrostis* (forms belonging to the *A. vulgaris* group). On an area burnt about 7 years ago, all the above occurred as scattered plants, but rarely play any important part in the vegetation. In the successions following the fire of 40 years ago exotics are virtually absent, and in the virgin vegetation an occasional plant of *Hypochaeris radicata* and *Holcus lanatus* may be found. On the old stock camp the following exotics were noted: *Agrostis* (as before) abundant, *Holcus lanatus, Anthoxanthum odoratum, Phleum pratense, Dactylis glomerata, Cerastium vulgatum, Rumex Acetosella, R. obtusifolius, Trifolium repens, Hypochaeris radicata* and *Lotus uliginosus.*

There are also, generally, large mats on the roadside of the indigenous species of *Acaena* and the hybrids between them; but, notwithstanding the special suitability of their hooked fruits for distribution by dogs, hares, sheep and man, and remembering the 70 years or so that the pass has been exposed

to their attacks, their occurrence in the indigenous vegetation is far from common. It may be that throughout New Zealand generally the presence of *Acaena* as a pasture weed is entirely due to settlement. As for the absence of exotics this fact should once more—*but this should not be needful*—bring home to biologists generally, that such plants cannot cope with indigenous plants, notwithstanding that for many years the contrary has formed part of the biological creed.

VI. Conclusion.

Here we do not present a summary of this paper since the facts detailed in section V, each under a distinct heading, appear concise enough, and would lose much of their meaning were they stated in fewer words. Nor have we given full details regarding the new communities, for this will be the aim of future papers. Our object has been to bring before ecological botanists in general a short account of the leading features of an unpremeditated experiment which man set in train many years ago. Such experiments occur in their thousands in the New Zealand region, where communities—primitive, mixed, indigenous-induced, exotic-induced, and artificial—grow perhaps side by side; and from such experiments lesson after lesson can be learnt which, if all were brought together, would do much to solve the questions concerning competition, succession, relation to habitat, the meaning of life forms and other matters which lie at the very basis of plant ecology. We have, generally, used throughout the term "Community" rather than the more definite term "Association" for the simple reason that we consider actual facts of superior importance to an attempted exactitude in terminology, and that we wish to avoid all ambiguity.

REFERENCES.

Cockayne, L. "On the burning and reproduction of subalpine scrub and its associated plants; with special reference to the Arthur's Pass district." *Trans. N.Z. Inst.* **31**, 398–419, 1899.

Cockayne, L. "A sketch of the plant geography of the Waimakariri River Basin, considered chiefly from an oecological point of view." *Trans. N.Z. Inst.* **32**, 95–136, 1900.

Cockayne, L. "On the occurrence of subalpine vegetation at a low level in the Fiord Botanical District (New Zealand) and other matters pertaining thereto." *Festschrift zum siebzigsten Geburtstage von Karl von Goebel in München.* Jena, 1925.

Cockayne, L. *Die Vegetation der Erde.* XIV. "The vegetation of New Zealand." Leipzig. 2nd ed., 1928.

THE BRYOPHYTES AND LICHENS OF MOORLAND

By W. WATSON.

(*With three Figures in the Text.*)

PREVIOUS articles on the cryptogams of various associations (**32**) appear to have been useful to ecologists, who have been dealing chiefly with phanerogamic vegetation, since frequent references have been made to them. No general paper dealing with the bryophytes and lichens of moorland in our islands has yet been published, though scattered references occur in a number of articles by myself and others (**8, 9, 13, 25, 32, 34**, etc.). Much of the work, of which the general results are given in this article, has been done, and partially prepared for publication, for some time, but its completion has been delayed by the stress of other work.

Moorland has a rather vague ecological meaning though it is often used as synonymous with heath. It is here used in a comprehensive way so that the bryophytes and lichens of various kinds of heath and moor can be dealt with. The rôle played by the lower plants on the constitution and succession of most ecological units is too important to be neglected, and one finds that much more attention is paid to them than was formerly the case. In many recent papers the ecological aspects of the bryophytes have been considered and in a few cases some account of the lichens has also been given. No general account of the algae or fungi of moorland has been attempted, though a few references to these plants are occasionally found (e.g. in **4, 11, 29, 32** *d, f, g*).

In the following list the bryophytes and lichens of sixteen heathlands are tabulated so as to give an idea of their respective frequencies. Most of the heathlands are dry ones and fuller particulars of them are given later. It must not be forgotten during the analysis of this list that wet heath has dry patches and that upland heath often merges into heather moor or even into some moister association. Upland heath, as here used in distinction from heather moor is drier, less acid, forms little peat and has a greater diversity of vascular plants (**30** *a*, pp. 98 *et seq.*, 208 *et seq.*). Transitions to heather moor are frequent, some of the Scottish moors described as upland heath have thick peat and some of the heather moors mentioned in this paper have been considered as upland heaths (**1**). Where such transitions are pronounced they have been neglected when the frequency has been valued for a particular association. In some cases then, a species may be frequent in the district, though its frequency value may be given as a low one in the list. For example, in most of the heaths listed *Polytrichum commune* is frequent but only in the wetter places. Its frequency is therefore given as a high value for the wet heaths but as a low one for the drier heaths. Its frequency, when the wetter

places are included, is given by the indicator in brackets, and when this method is adopted the plant is rare or absent on the typical portions of the heathland. In some cases further information of a qualifying nature is given by means of the notes referred to by the letters in the last column.

There is no attempt made to give a complete list of the spermophytes and pteridophytes. Some are listed in order that the phanerogamic ecologist may form a general idea of the kind of heathland on which the bryophytes and lichens listed occur. On some of the heathlands the vascular plants were not fully investigated in regard to their frequencies and therefore only their presence is indicated.

The first five heaths (*A–E*) are in Somerset and are chiefly dominated by *Calluna*, though *Ulex* and *Pteris* may be locally dominant. Those on the Quantock hills (*A*) and Exmoor (*D*) are on siliceous rocks of the Devonian system. A little Carboniferous Limestone occurs but the heath is not present on this unless considerable leaching has occurred. The heath on the Brendon hills (*B*) is on siliceous soil of the Devonian, Permian and Triassic systems, that on the Blackdowns (*C*) is on Greensand or on other Cretaceous beds from which all the chalk has been washed out leaving a deposit of flints and clay. The Mendip heath (*E*) is on Old Red Sandstone fringed by Carboniferous limestone on which the heath does not encroach unless considerable leaching has occurred. On both Mendip and Exmoor the upland heaths show transitions to heather moor. The altitude of these Somerset heathlands is about 800–1000 ft., though the highest parts of the Quantocks (Will's Neck) reaches 1260 ft., of the Brendons 1300 ft., whilst on Exmoor heath formation is common at 1400–1500 ft. and even reaches almost to the highest point (Dunkery Beacon) at 1708 ft. At or near the summits of the hills these uplands are often of a wetter character and the association sometimes becomes nearer to that of high moor or sometimes is of a more open character approximating to that found in subalpine or alpine localities. Trees are few or absent, except in the combes or valleys, and the bryophytes or lichens occurring in these have not been included, unless they also occur on the heath. Rock surfaces are seldom present except when due to human agency, and the saxicolous cryptogams listed occur on small stones scattered on the heath.

The next seven moorlands (*F–L*) represent heather moors. In all of them rock surfaces occur, boulders being especially frequent on the Dartmoor (*F*), Snowdon (*J*), Perthshire (*K*) and Brecon (*L*) heaths. The Dartmoor area studied is chiefly on granitic rock fringed by some Devonian slates. The vegetation on the latter is not of such variety as on the granite. The area is given as a heather moor but it often merges into upland heath, wet heath or high moor (hochmoor). On the Minera Mt in Denbigh (*G*) the underlying substratum is Millstone Grit with some arenaceous Ordovician beds at the highest point. Some Carboniferous Limestone is present in the fringing portions and in a rocky glen where a mixed flora is found as both calcareous and siliceous

rocks are present (**32** *g*, p. 191). The other heathlands are on siliceous or metamorphic rocks. The moors of the Pennines (*I*) overlie Millstone Grit, those of the Brecons (*L*) Devonian siliceous rocks and those of Cannock Chase (*H*) are on Carboniferous and Keuper sandstones and shales. Near Llanberis (Snowdon) the heathlands are chiefly on Cambrian and Ordovician shales and sandstones with some volcanic rock (*J*); near Killin (*K*) chiefly on metamorphic rock with some morainic débris. Both in the Killin and Llanberis districts some calcium-containing rocks are present, but the plants of such areas are not included in the general list. When included elsewhere the possibility of the presence of calcium is specially mentioned.

The last four heaths (*M–P*) are wet heaths at low altitudes. They occur on sandy or peaty soil which are chiefly alluvial deposits. It is therefore of little importance to state the underlying geological formation. Some of the sandy soils of the Bagshot heaths (*O*) are of Tertiary date, whilst in the other three they are chiefly post-Tertiary. Exposed rock surfaces are absent except on the Studland heath (included in *O*), and the saxicolous plants given in the list occur on small stones. Trees, especially birch, are present on some parts, but the bryophytes or lichens on or under them are not included in the list unless they also occur on the unshaded portions. There seems to be little reason to include them, since their occurrence does not depend directly on the nature of the underlying soil, and also because similar conditions on other soils than heathland cause the same associations to occur. Atmospheric conditions, such as the relative purity of the air, influence the development of corticicolous epiphytes to a much greater extent than they do that of terrestrial or saxicolous cryptogams. There is, however, some slight dependence on the nature of the soil, since the latter is correlated with the absence or presence of various trees which influence the development of the epiphytes. For example, the smooth bark of the beech is the favourite habitat of some species of *Graphis*, *Arthonia*, etc., though these are not confined to the beech. They have been noted on various trees and have even been found on oaks when they were young and had smooth bark. The conifers and birches sometimes have a fairly well-defined epiphytic association, but the exceptions to such a definite correlation between the tree and its epiphytes are so numerous that it is considered inadvisable to include corticicolous plants in the tabulated list.

The frequencies are denoted by the usual abbreviations: a., abundant; f., frequent; o., occasional; r., rare. When d. is used the plant tends to become the dominant member in the smaller plant world, whilst l. expresses the frequency in a local area. In some cases the frequency is unknown or doubtful and the presence of the plant is indicated by a short horizontal line. The lack of definiteness in such cases is usually due to the difficulties of distinguishing such small plants in the field, though the frequency can rarely be of a higher order than o. Some plants which are listed are of common occurrence on heaths but are more characteristic of certain portions, and special references

are often added so as to direct attention to this. For example, *Polytrichum aloides* is frequently found on heathlands but usually occurs on their banks by the sides of paths, etc. Again, *Eurhynchium praelongum* is occasionally found on the actual moorland but cannot be considered as a characteristic member though it is often frequent in marginal associations. By such methods an attempt has been made to show the "selective power" of the association. It is, however, very difficult to express in a brief manner the fine shades of distinction between the various facies of an association. Therefore the frequencies must be considered as referring to the peaty ground unless special notes are given. In many cases the frequency is much greater if the plants on trees or large rocks are considered. Those which occur on trees only are not included, whilst the frequencies given for saxicolous plants usually refer to their occurrence on small stones scattered over the surface of the heath.

LIST OF PLANTS FROM SIXTEEN MOORLANDS.

Explanation of abbreviations used in the list.

A E. Upland heaths of Somerset: *A*, Quantocks; *B*, Brendons; *C*, Blackdowns near Taunton; *D*, Exmoor; *E*, Mendip.

F L. Heather moors: *F*, Dartmoor (near Widecombe); *G*, Minera Mt, Denbigh; *H*, Cannock Chase, Staffordshire; *I*, Southern Pennines; *J*, Snowdonia (near Llanberis); *K*, Perthshire (near Killin); *L*, Brecon beacons (lower slopes).

M-P. Wet heaths: *M*, Shapwick turf moor, Somerset; *N*, Skipwith Common, Yorkshire; *O*, heaths of the Bagshot beds in East Dorset and West Hampshire; *P*, Delamere Forest, Cheshire.

Frequency indicators: d., dominant; a., abundant; f., frequent; o., occasional; r., rare; l., local; –, present but of doubtful frequency. Bracketed indicator shows the frequency in a less typical part of the heathland.

References in the last column: These refer to the following special notes in regard to habitat, etc. In such habitats the plant is sometimes more frequent than is indicated in the list. b., banks; bg., boggy places; bo., usually on boulders; b.s., banks or stony ground; c., on ling; d.p., damp portions of the moorland; d.r., damp rock; e., chiefly the form *pleolepidea*; g., grassy places or heathy pasture; g.b., grassy or mossy banks; h., heap of small stones; i., more frequent on damp moorland especially var. *cetrariaeformis*; l.t., on ling, frequent on trees in most of the localities; m.a., often frequent in marginal associations; mo., frequent in moist places; m.r., mossy rocks; n., in nooks; pa., damp stony paths; pi., frequent near firs; ro., usually on rocks; sa., often on sandy places; s.c., soil-capped rocks; sh., shaded places; sp., usually amongst *Sphagnum*; st., on stones; t., frequent on trees; t.b., especially at bases of trees; u., varieties *pinnata* and *recurva* occur in shadier or damper situations; v., chiefly the form *trachypoda*; w., wet places; w.r., wet rocks; x., this includes several segregates; y., on bryophytes.

Nomenclature: Spermophyta and Pteridophyta *sec. London Catalogue*, 11th edition. Bryophyta *sec.* the *Census Catalogues of the British Bryological Society*. The species of *Hypnum* are often distributed amongst various genera, but this course has been followed only in the case of *Drepanocladus*. All the records for *Cephaloziella bifida* probably belong to *C. hampeana*, but as the plants were determined before the relationship of these names were understood the former name has been kept in the list. Lichens chiefly according to the British Museum Monographs (A. L. Smith) with some modifications in generic names in accordance with my *Classification of Lichens*.

	Upland heaths of Somerset					Heather moors							Wet heaths				
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Notes
Viola canina	o.	.	o.	r.	.	–	.	.	.	–	l.	.	o.	.	r.	–	
V. lactea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	f.	–	
Polygala serpyllacea	f.	f.	f.	f.	f.	f.	f.	f.	o.	o.	f.	–	a.	f.	o.	o.	
Radiola linoides	r.	.	r.	.	.	.	.	.	.	.	.	.	f.	–	f.	r.	
Linum catharticum	o.	o.	o.	o.	i.	o.	.	.	o.	o.	f.	–	f.	f.	f.	o.	
Rhamnus frangula	r.	r.	r.	o.	f.	.	.	.	.	.	.	.	f.	o.	f.	.	
Genista anglica	.	r.	r.	r.	.	.	.	r.	.	.	.	.	.	.	f.	.	
Ulex europaeus	f.	f.	f.	f.	f.	f.	f.	f.	o.	o.	o.	o.	f.	f.	f.	l.a.	
U. gallii	a.	a.	f.	a.	f.	a.	.	.	o.	o.	.	.	f.	.	f.	o.	
U. minor	.	.	r.	r.	.	.	.	.	.	.	.	.	r.	.	a.	.	
Cytisus scoparius	r.	r.	.	.	r.	–	–	r.	–	f.	–	.	o.	–	f.	l.a.	
Potentilla erecta	f.	f.	f.	f.	f.	a.	f.	f.	o.	f.	f.	f.	f.	f.	f.	f.	
P. palustris	.	.	.	.	.	.	–	–	–	.	.	o.	a.	–	f.	o.	
Drosera anglica	.	.	(o.)	(o.)	.	(o.)	.	.	.	(r.)	(o.)	.	r.	.	r.	o.	w.
D. rotundifolia	(o.)	(o.)	(f.)	(o.)	(o.)	(f.)	(–)	(o.)	(r.)	(f.)	(f.)	(f.)	l.a.	l.a.	l.a.	f.	w.
D. longifolia	.	.	(o.)	.	(o.)	.	.	(o.)	.	(r.)	.	.	f.	o.	f.	o.	w.
Galium saxatile	f.	f.	f.	f.	f.	f.	a.	f.	o.	f.	f.	f.	f.	f.	f.	f.	
Vaccinium myrtillus	l.f.	l.f.	o.	l.f.	o.	a.	f.	l.a.	l.a.	l.a.	l.f.	l.f.	r.	o.	o.	l.a.	
V. vitis-idaea	r.	.	.	.	.	.	.	o.	o.	o.	.	.	.	.	.	.	
Oxycoccus quadripetala	.	(r.)	(r.)	(r.)	(r.)	.	(r.)	(r.)	.	(l.)	.	.	r.	.	.	.	mo.
Andromeda polifolia	.	.	.	.	(r.)	.	.	(r.)	.	.	.	.	r.	.	.	o.	mo.
Calluna vulgaris	l.d.	a.	a.	l.d.	l.d.	a.	a.	a.	a.	f.	f.	a.	l.d.	l.a.	l.a.	l.d.	
Erica ciliaris	.	.	.	.	.	.	.	.	.	.	.	.	.	r.	.	.	
E. tetralix	r.	r.	r.	o.	(f.)	a.	f.	o.	f.	f.	f.	f.	l.a.	a.	l.a.	o.	mo.
E. cinerea	f	f.	f.	f.	f.	a.	a.	a.	a.	a.	a.	a.	o.	o.	o.	l.d.	
Anagallis tenella	(f.)	(f.)	(f.)	(f.)	(o.)	f.	–	–	–	–	–	r.	f.	r.	a.	r.	mo.
Gentiana pneumonanthe	.	.	.	.	.	.	.	.	.	.	.	.	.	f.	f.	.	
Veronica serpyllifolia	f.	f.	f.	f.	f.	o.	o.	o.	o.	o.	–	–	f.	–	f.	f.	
Pedicularis palustris	(o.)	(o.)	(o.)	(o.)	(o.)	(f.)	–	–	(o.)	–	(f.)	–	f.	.	f.	o.	mo.
P. sylvatica	f.	f.	f.	f.	f	f.	–	f.	o.	–	f.	–	a.	–	f.	f.	
Melampyrum pratense	f.	o.	f.	r.	f.	f.	–	o.	o.	–	o.	–	r.	r.	o.	.	
Pinguicula vulgaris	.	.	.	.	.	.	–	–	(r.)	–	(f.)	–	r.	–	r.	.	mo.
P. lusitanica	.	.	o.	o.	o.	.	.	.	.	.	.	.	o.	.	o.	.	mo.
Rumex acetosella	f.	f.	f.	f.	o.	f.	–	f.	f.	–	f.	.	f.	–	f.	a.	
Myrica gale	.	.	o.	.	.	.	.	.	.	o.	o.	.	l.f.	–	f.	r.	mo.
Betula alba	o.	o.	o.	o.	o.	o.	–	o.	f.	–	f.	.	o.	f.	f.	l.a.	
B. pubescens	o.	o.	f.	f.	o.	–	–	o.	o.	o.	f.	.	f.	f.	f.	f.	
Empetrum nigrum	r.	.	.	o.	.	.	.	o.	f.	o.	o.	.	.	.	f.	r.	
Juncus bufonius	(f.)	(f.)	(f.)	(f.)	(f.)	f.	–	f.	f.	f.	f.	f.	a.	f.	f.	f.	mo.
J. squarrosus	f	o.	o.	f.	o.	f.	–	a.	a.	f.	f.	f.	f.	f.	f.	f.	
J. inflexus	(f.)	(f.)	(f.)	(f.)	(f.)	f.	f.	o.	f.	–	r.	.	a.	f.	f.	o.	mo.
J. effusus	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(o.)	(o.)	(f.)	(f.)	(f.)	(f.)	a.	f.	f.	f.	w.
Luzula pilosa	f.	f.	f.	a.	f.	f.	.	–	f.	l.f.	–		f.	–	f.	f.	
L. multiflora	o.	o.	o.	f.	f.	o.	–	–	o.	f.	–		f.	–	f.	f.	
Eleocharis multicaulis	.	.	(o.)	(o.)	(o.)	.	.	.	.	.	r.	.	f.	–	a.	o.	
Scirpus caespitosus	f.	o.	f.	l.a.	f.	f.	–	f.	f.	f.	f.	f.	f.	–	a.	f.	
Eriophorum vaginatum	(r.)	(o.)	(o.)	(r.)	(o.)	(o.)	–	o.	l.f.	r.	o.	.	o.	–	l.r.	o.	mo.
E. angustifolium	(o.)	(o.)	(f.)	(f.)	(o.)	(f.)	(–)	(–)	(o.)	(f.)	(f.)	(–)	a.	–	a.	o.	w.
Rhynchospora alba	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	–	(o.)	.	.	.	.	l.f.	–	o.	o.	mo.
Carex pulicaris	(f.)	(f.)	(f.)	(f.)	(o.)	f.	–	–	l.f.	l.f.	.		f.	.	f.	.	d.p.
C. echinata	(f.)	(f.)	(f.)	(f.)	(f.)	f.	.	f.	.	f.	f.	.	f.	–	a.	f.	mo.
C. panicea	(o.)	(f.)	(f.)	(f.)	(f.)	f.	–	f.	.	f.	f.	f.	f.	–	f.	f.	d.p.
C. binervis	o.	o.	o.	f.	f.	f.	–	.	o.	f.	.	.	f.	–	f.	o.	d.p.
Anthoxanthum odoratum	f.	f.	f.	f.	f.	f.	–	o.	o.	o.	o.	.	f.	o.	o.	f.	
Agrostis setacea	a.	a.	a.	a.	.	.	.	.	.	.	.	.	.	.	a.	.	
A. canina	o.	f.	o.	f.	o.	f.	.	.	.	.	.	.	f.	–	f.	.	
A. tenuis	a.	a.	a.	a.	a.	a.	–	f.	o.	f.	f.	f.	a.	f.	f.	f.	
Aira caryophyllea	o.	o.	o.	o.	o.	o.	.	.	–	.	–	–	o.	–	f.	o.	
A. praecox	o.	r.	r.	f.	o.	f.	.	.	–	.	–	–	o.	.	f.	o.	
Deschampsia flexuosa	a.	a.	a.	a.	f.	f.	–	f.	f.	f.	f.	f.	f.	f.	r.	f.	
Sieglingia decumbens	o.	o.	o.	o.	o.	o.	–	.	.	f.	l.	–	f.	.	f.	f.	d.p.
Molinia coerulea	l.a.	.	l.a.	l.a.	.	a.	–	l.a.	l.f.	f.	f.	f.	l.a.	l.a.	f.	f.	d.p.
Festuca ovina	a.	a.	a.	a.	a.	a.	–	f.	f.	f.	f.	f.	f.	f.	f.	–	d.p.
Nardus stricta	l.f.	l.f.	l.f.	l.a.	l.a.	f.	–	f.	o.	f.	f.	f.	f.	f.	o.	f.	
Pteris aquilina	l.a.	l.a.	l.a.	l.a.	l.f.	l.f.	l.f.	l.a.	l.a.	f.	f.	f.	l.a.	l.a.	l.a.	l.d.	
Blechnum spicant	o.	o.	o.	o.	o.	f.	–	.	a.	f.	f.	f.	f.	.	l.f.	o.	b.
Lastrea thelypteris	.	.	.	.	.	.	.	.	.	.	.	.	a.	.	r.	.	
Osmunda regalis	.	.	.	.	.	.	.	.	.	.	(r.)	.	l.f.	r.	r.	r.	
Lycopodium selago	r.	r.	r.	r.	.	o.	–	–	.	o.	o.	.	.	.	r.	.	
L. clavatum	o.	o.	r.	o.	r.	f.	–	–	.	f.	o.	.	.	r.	r.	.	
Tetraphis pellucida	o.	o.	–	o.	o.	o.	f.	f.	f.	f.	f.		–	–	o.	.	b.

	Upland heaths of Somerset					Heather moors							Wet heaths				Notes
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	
Catharinea undulata	f.	f.	f.	f.	f.	f.	-	f.	f.	f.	f.	f.	.	.	o.	-	b.
Oligotrichum hercynicum	.	.	.	.	.	.	-	-	f.	f.	f.	f.	.	.	.	-	d.p.
Polytrichum nanum	r.	r.	r.	r.	r.	o.	-	-	.	o.	-	-	.	.	o.	o.	b.s.
P. aloides	f.	f.	o.	f.	o.	f.	-	-	o.	f.	f.	-	.	.	f.	-	b.s.
P. urnigerum	o.	o.	o.	o.	o.	o.	-	-	o.	o.	o.	o.	.	.	f.	-	b.s.
P. piliferum	a.	a.	f.	a.	f.	a.	a.	a.	-	a.	a.	a.	.	.	f.	f.	
P. juniperinum	a.	a.	a.	a.	a.	a.	a.	-	f.	f.	-	f.	a.	a.	a.	-	
P. strictum	.	.	.	.	.	o.	-	o.	o.	-	o.	-	.	o.	o.	-	d.p.
P. alpinum	.	.	.	.	.	r.	.	.	o.	o.	o.	o.	.	.	.	.	
P. gracile	.	.	o.	.	o.	o.	-	-	o.	o.	o.	o.	-	-	.	o.	
P. formosum	a.	a.	a.	a.	a.	a.	a.	f.	f.	f.	f.	a.	f.	f.	a.	f.	sh.
P. commune	(f.)	(f.)	(f.)	(f.)	(f.)	(a.)	(a.)	(a.)	(a.)	(a.)	(a.)	(a.)	a.	a.	a.	a.	w.
Diphyscium foliosum	.	.	.	o.	.	o.	.	-	-	-	o.	.	.	.	.	.	b.
Pleuridium subulatum	o.	o.	o.	o.	o.	o.	.	-	o.	o.	-	o.	.	-	o.	o.	b.
Ditrichum homomallum	o.	o.	.	o.	o.	o.	-	-	o.	o.	o.	-	.	.	.	-	sa.
Swartzia montana	.	.	.	.	.	.	.	-	o.	o.	o.	-	.	.	.	.	ro.
Ceratodon purpureus	a.	a.	a.	a.	a.	a.	a.	a.	a.	a.	a.	a.	a.	f.	a.	-	
Dicranella heteromalla	a.	a.	a.	a.	f.	a.	a.	a.	a.	a.	a.	a.	a.	f.	a.	a.	
D. cerviculata	o.	o.	o.	o.	o.	o.	o.	-	o.	o.	o.	o.	f.	o.	.	-	
Campylopus flexuosus	a.	a.	a.	f.	f.	f.	f.	f.	a.	f.	f.	f.	-	-	a.	f.	
C. pyriformis	a.	f.	f.	f.	f.	f.	f.	a.	a.	f.	f.	f.	.	a.	a.	a.	
C. fragilis	r.	r.	r.	o.	-	o.	-	o.	o.	o.	-	-	o.	-	o.	-	
C. atrovirens	.	.	.	.	.	o.	-	.	o.	f.	f.	-	.	f.	o.	.	mo.
C. brevipilus	.	.	.	.	.	r.	.	-	-	-	-	-	o.	a.	a.	-	mo.
C. subulatus	.	.	o.	.	.	.	.	.	.	-	-	-	o.	.	.	.	
Dicranum scoparium	a.	a.	f.	a.	f.	a.	f.	f.—a.	f.	a.	a.	f.	a.	f.	a.	a.	
D. bonjeani	o.	.	o.	.	-	-	-	-	-	-	-	-	.	f.	f.	-	d.p.
D. spurium	.	.	.	.	.	r.	.	-	-	.	.	o.	.	o.	o.	-	d.p.
Leucobryum glaucum	(o.)	(o.)	(o.)	(o.)	(o.)	o.	-	o.	o.	f.	f.	o.	f.	f.	a.	..	d.p.
Rhacomitrium canescens	o.	o.	o.	f.	o.	f.	f.	-	-	f.	f.	-	.	.	.	.	sa.
R. heterostichum	o.	o.	-	o.	.	f.	o.	-	o.	f.	f.	o.	.	.	.	.	ro.
R. fasciculare	.	.	.	o.	r.	o.	-	-	-	f.	f.	-	.	.	.	.	ro.
R. lanuginosum	o.	o.	o.	o.	o.	a.	f.	-	o.	a.	a.	f.	-	f.	-		
Fissidens adiantoides	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	-	(o.)	(o.)	(o.)	(o.)	-	f.	f.	-	mo.
Leptodontium flexifolium	.	r.	r.	.	o.	o.	o.	o.	-	o.	.	.	.	.	o.	.	
Funaria hygrometrica	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	-	
Aulacomnium palustre	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	f.	a.	a.	f.	w.
A. androgynum	.	o.	.	o.	.	r.	-	o.	..	.	.	.	f.	o.	o.	o.	
Bartramia pomiformis	f.	f.	f.	f.	o.	f.	o.	-	-	o.	f.	o.	.	.	.	o.	
Philonotis fontana	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	-	(f.)	(f.)	(f.)	f.	f.	f.	f.	mo.
Orthodontium heterocarpum	.	.	.	.	.	.	.	.	o.	.	.	.	.	.	.	.	
Webera nutans	a.	a.	f.	a.	f.	a.	f.	f.	a.	a.	a.	f.	a.	a.	a.	f.	
Bryum pendulum	-	-	-	-	-	-	-	-	o.	-	-	-	.	.	.	-	b.
B. inclinatum	o.	-	-	-	o.	o.	o.	-	o.	o.	-	-	.	.	.	-	b.
B. pallens	o.	o.	o.	o.	o.	o.	o.	-	o.	o.	o.	o.	.	o.	.	..	
B. capillare	o.	o.	o.	o.	o.	o.	o.	o.	o.	f.	f.	f.	a.	f.	f.	-	
B. atropurpureum	.	o.	.	.	o.	-	-	-	-	-	-	-	.	.	o.	.	
B. erythrocarpum	o.	-	o.	-	o.	-	-	o.	o.	-	-	-	.	.	.	.	
B. pseudotriquetrum	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	o.	o.	o.	-	mo.
B. bimum	.	.	.	(o.)	(o.)	(o.)	(o.)	.	.	.	.	.	o.	.	o.	o.	mo.
B. roseum	r.	r.	.	r.	o.	o.	-	r.	r.	r.	r.		r.	.	.	.	
Mnium affine	o.	o.	o.	-	o.	o.	.	-	o.	o.	o.		-	.	.	.	b.
M. cuspidatum	o.	o.	o.	o.	o.	o.	o.	-	o.	-	-	-	.	.	.	.	b.
M. undulatum	f.	f.	f.	f.	f.—a.	f.	f.	f.	f.	o.	o.	o.	f.	f.	f.	f.	b.
M. hornum	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	a.	f.	a.	-	b.
M. serratum	.	.	.	.	.	r.	o.	-	r.	o.	o.	r.	.	.	.	.	
Thuidium tamariscinum	f.	f.	o.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	.	
Climacium dendroides	.	.	o.	o.	o.	o.	o.	-	o.	o.	o.	o.	f.	o.	f.	-	
Brachythecium purum	a.	a.	a.	a.	f.	a.	f.	-	f.	f.	f.	f.	f.	f.	f.	.	
B. rutabulum	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	m.a.
B. velutinum	o.	o.	o.	o.	f.	f.	f.	-	o.	o.	-	-	o.	o.	o.	.	m.a.
Eurhynchium myosuroides	f.	f.	f.	f.	f.	a.	f.	-	o.	f.	o.	f.	o.	-	o.	.	m.a.
E. praelongum	o.	o.	o.	o.	f.	o.	f.	o.	o.	o.	o.	o.	o.	o.	.	o.	m.a.
Plagiothecium elegans	f.	o.—f.	.	f.	f.	f.	f.	f.	f.	f.	f.	f.	.	.	.	.	n.
P. denticulatum	o.	o.	o.	o.	o.	f.	-	o.	o.	o.	f.	o.	.	.	.	.	b.
P. silvaticum	r.	r.	r.	r.	o.	o.	-	o.	o.	o.	o.	o.	.	.	.	.	b.
P. undulatum	o.	o.	o.	o.	o.	f.	o.	f.	o.	o.	o.	o.	.	.	.	f.	sh.
Drepanocladus aduncus	.	.	.	.	.	(a.)	.	.	.	.	.	.	f.	a.	.	f.	w.
D. exannulatus	.	(o.)	.	(f.)	.	(o.)	(-)	(-)	(o.)	(o.)	(o.)	(o.)	o.	f.	o.	o.	w.
D. fluitans	.	.	(o.)	(o.)	(o.)	(f.)	(-)	(f.)	(o.)	(o.)	(o.)	(o.)	o.	f.	-		w.
D. uncinatus	.	.	.	.	.	o.	.	.	o.	o.	o.	-	.	o.	-	.	

	Upland heaths of Somerset					Heather moors							Wet heaths				Notes
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	
D. sendtneri	.	.	.	.	.	o.	.	-	o.	.	.	.	.	o.	.	.	mo.
Hypnum cupressiforme	o.	o.	o.	o.	.	o.	o.	o.	f.	f.	f.	f.	f.	a.	a.	f.	
var. ericetorum	a.-d.	a.	a.	a.-d.	a.	a.	a.	a.	a.	a.	a.	a.	a.	a.	a.	a.	
H. imponens	.	.	.	.	.	r.	.	.	.	.	o.	.	.	o.	o.	.	
H. stramineum	(o.)	(o.)	(o.)	(o.)	.	o.	.	.	o.	o.	o.	o.	.	-	o.	o.	mo.
H. schreberi	a.	o.	f.	a.	a.	a.	f.	f.	o.	f.	f.	f.	f.	.	-	f.	
H. cuspidatum	(o.)	(o.)	(o.)	(o.)	(o.)	o.	o.	o.	o.	o.	o.	o.	a.	a.	a.	a.	mo.
Hylocomium splendens	a.	a.	a.	a.	a.	a.	f.	f.	o.	f.	f.	f.	f.	f.	f.	f.	
H. loreum	o.	o.	o.	o.	.	f.	f.	-	o.	f.	f.	f.	.	.	f.	.	
H. squarrosum	l.a.	f.	l.a.	f.	f.	f.	f.	f.	a.	f.	f.	f.	-	-	o.	a.	g., pi.
H. triquetrum	o.	o.	f.	o.	f.	f.	f.	f.	o.	f.	f.	f.	.	.	o.	f.	sh.
Marchantia polymorpha	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	-	f.	o.	o.	o.	mo.
Aneura pinguis	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	(o.)	-	(o.)	(o.)	(f.)	(o.)	.	.	o.	-	mo.
Pellia epiphylla	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	(f.)	f.	f.	o.	f.	w.
P. fabbroniana	(r.)	(r.)	(o.)	(r.)	(o.)	(r.)	(o.)	.	(o.)	(o.)	.	(o.)	o.	-	f.	.	w.
Fossombronia dumortieri	.	.	.	.	.	.	.	.	.	.	.	.	.	o.	.	.	
Marsupella ustulata	.	.	.	.	.	.	.	.	o.	o.	.	.	.	.	.	.	
M. funckii	.	.	.	.	.	.	.	.	o.	r.	.	.	.	.	.	.	pa.
M. emarginata	r.	r.	.	f.	.	o.	o.	-	o.	o.	o.	o.	.	.	.	.	w.r.
Alicularia scalaris	f.	f.	.	f.-a.	.	o.	f.	f.	f.	f.	f.	f.	.	f.	o.	.	d.p.
A. geoscypha	.	.	r.	r.	.	-	.	.	.	.	o.	.	.	f.	.	o.	d.p.
Eucalyx hyalinus	o.	.	.	o.	r.	o.	o.	-	o.	.	o.	.	.	.	.	.	
Aplozia crenulata	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	.	.	o.	.	sh.
Gymnocolea inflata	(o.)	(o.)	(o.)	(f.)	(o.)	(f.)	(o.)	(f.)	(f.)	(f.)	(f.)	(o.)	a.	a.	a.	f.	bg.
Lophozia ventricosa	o.	o.	o.	o.	o.	f.	o.	o.	o.	f.	f.	o.	.	o.	o.	o.	d.p.
L. bicrenata	.	r.	.	r.	.	r.	.	-	o.	.	r.	-	.	.	.	o.	
L. excisa	.	o.	o.	.	.	.	.	-	o.	o.	.	-	.	.	.	o.	sh.
L. floerkii	.	.	.	r.	.	r.	f.	-	f.	f.	f.	.	.	.	.	-	
L. atlantica	.	.	.	.	.	.	.	.	o.	o.	.	.	.	.	.	.	ro.
L. attenuata	.	.	r.	.	.	r.	o.	-	o.	o.	o.	.	.	.	.	.	sh.
Sphenolobus minutus	.	.	.	.	.	.	.	.	o.	o.	.	.	.	.	.	.	ro.
S. exsectiformis	.	r.	r.	r.	.	-	.	.	o.	o.	.	.	.	.	.	o.	
Plagiochila asplenioides	o.	o.	o.	o.	o.	o.	.	o.	o.	o.	o.	o.	o.	o.	o.	o.	sh.
Leptoscyphus taylori	.	.	.	.	.	.	-	-	f.	f.	f.	f.	.	.	.	.	d.p.
L. anomalus	.	.	.	.	.	.	.	o.	.	.	o.	.	.	o.	o.	o.	d.p.
Lophocolea bidentata	o.	o.	o.	o.	o.	o.	o.	o.	f.	f.	f.	f.	o.	o.	o.	o.	m.a.
Cephalozia bicuspidata	f.	o.	o.	f.	o.	f.	f.	f.	f.	f.	f.	f.	a.	a.	a.	a.	d.p.
C. connivens	r.	r.	r.	r.	.	o.	.	o.	f.	o.	o.	o.	.	f.	f.	-	mo.
C. macrostachya	.	.	.	.	.	.	.	.	.	.	o.	.	.	.	a.	.	mo.
C. franscisci	.	.	.	.	.	.	.	.	.	.	o.	.	.	o.	o.	.	
C. media	r.	o.	.	o.	.	-	o.	.	r.	o.	o.	-	.	.	.	-	sh.
C. leucantha	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
C. fluitans	.	.	.	.	.	.	.	.	.	r.	r.	.	.	.	o.	o.	w.
Cephaloziella starkii	f.	f.	f.	f.	o.	f.	f.	a.	a.	f.	f.	f.	f.	a.	a.	f.	d.p.
C. bifida	.	o.	.	.	.	-	o.	-	o.	o.	o.	-	f.	o.	f.	f.	d.p.
Calypogeia trichomanis	f.	f.	o.	f.	o.	f.	f.	f.	f.	f.	f.	-	f.	f.	a.	-	d.p.
C. fissa	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	b.
C. arguta	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	n.
Lepidozia reptans	f.	f	o.	f.	o.	f.	f.	f.	f.	f.	f.	-	f.	f.	f.	.	d.p.
L. trichoclados	.	.	.	r.	.	.	.	.	.	.	.	.	.	.	.	.	mo.
L. setacea	.	.	r.	r.	r.	-	-	o.	o.	o.	-	.	f.	f.	f.	.	w.
Ptilidium ciliare	o.	o.	.	o.	.	o.	-	o.	.	f.	f.	.	.	.	.	f.	d.p.
Diplophyllum albicans	f.	f.	f.	f.	f.	f.	f.	f.	f.	a.	a.	a.	o.	o.	o.	-	
Scapania compacta	o.	o.	.	o.	.	o.	o.	-	o.	o.	o.	.	.	.	.	.	
S. curta	o.	o.	o.	o.	.	o.	o.	o.	o.	o.	o.	.	o.	.	.	-	g.
S. umbrosa	.	.	o.	.	.	o.	-	o.	o.	o.	o.	.	.	.	.	.	
Frullania tamarisci	f.	f.	o.	f.	f.	f.	f.	o.	o.	f.	f.	f.	.	.	.	.	ro.
Odontoschisma sphagni	(o.)	.	.	(o.)	.	(o.)	.	(o.)	-	(o.)	(o.)	(o.)	.	o.	o.	o.	sp.
O. denudatum	.	.	.	.	.	.	.	.	.	.	.	.	.	o.	o.	o.	mo.
Usnea florida	.	.	.	.	.	.	.	.	.	.	.	.	o.	o.	o.	.	l.t.
Alectoria chalybeiformis	.	.	.	.	.	o.	.	.	.	o.	f.	.	.	.	.	.	m.r.
A. bicolor	.	.	.	.	.	o.	.	.	.	f.	f.	.	.	.	.	.	ro.
Parmelia fuliginosa	o.	o.	o.	o.	o.	o.	-	o.	.	o.	o.	o.	.	.	.	.	st., t.
P. saxatilis	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	o.	o.	f.	-	st., t.
P. omphalodes	.	.	o.	.	.	f.	o.	f.	o.	f.	f.	f.	.	.	.	.	ro.
Hypogymnia physodes	f.	o.	o.	f.	f.	f.	o.	f.	o.	f.	o.	o.	o.	o.	f.	f.	l.t.
H. vittata	r.	.	r.	.	.	.	.	.	.	.	o.	.	.	o.	.	.	
Cetraria islandica	.	.	.	.	.	.	.	.	.	f.	f.	.	.	o.	.	.	
var. tenuifolia	.	.	.	.	.	.	.	.	.	-	-	.	.	o.	.	.	
C. aculeata	f.	f.	f.	f.	o.	f.	o.	f.	o.	f.	f.	f.	.	f.	a.	f.	
var. hispida in drier places																	

	Upland heaths of Somerset					Heather moors							Wet heaths				Notes
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	
Lecanora polytropa	f.	f.	o.	f.	o.	f.	o.	–	o.	f.	f.	f.	.	.	o.	.	st.
L. varia	o.	o.	o.	o.	–	o.	.	.	.	.	.	.	f.	.	f.		l.t.
Psora demissa	.	.	.	.	.	.	.	.	.	o.	o.	.	.	.	.	.	
Biatora coarctata	f.	o.	o.	f.	o.	f.	.	.	–	f.	f.	f.	.	.	o.	.	st.
B. granulosa	a.	a.	f.	a.	f.	a.	.	f.	f.	f.	f.	f.	.	f.	f.	o.	
B. gelatinosa	.	.	.	.	.	.	.	.	.	.	r.	.	.	.	r.	.	
B. uliginosa	a.	a.	a.	a.	f.	a.	f.	a.	–	a.	a.	f.	.	f.	f.	f.	
Lecidea lithophila	.	.	r.	r.	r.	o.	–	.	.	o.	o.	.	.	.	.	.	h.
L. rivulosa	f.	.	o.	a.	.	a.	–	.	.	a.	a.	f.	.	.	.	.	st.
L. kochiana	.	.	.	.	.	.	.	.	.	f.	–	f.	.	.	.	.	st.
L. lygea	.	.	.	r.	.	.	.	.	.	f.	–	f.	.	.	.	.	st.
L. contigua	a.	a.	a.	a.	a.	a.	a.	–	f.	a.	a.	a.	o.	o.	a.	–	st.
L. sorediza	a.	a.	f.	a.	f.	a.	.	.	.	f.	f.	f.	.	.	.	.	st.
L. crustulata	o.	o.	o.	o.	o.	o.	.	.	.	f.	f.	.	.	o.	.	.	h.
L. dicksonii	.	.	.	o.	.	–	.	.	–	f.	f.	.	.	.	.	.	h.
L. sylvicola	o.	.	o.	o.	o.	.	.	.	.	o.	–	.	.	.	.	.	h.
L. expansa	o.	.	.	.	.	–	.	.	.	–	.	o.	.	.	.	.	h.
Pertusaria dealbata	f.	f.	o.	f.	o.	f.	.	f.	–	f.	f.	f.	.	.	.	–	h.
Acarospora fuscata	.	.	o.	o.	o.	o.	.	.	.	o.	–	o.	.	.	.	.	st.
Biatorina littorella	o.	.	o.	.	.	.	.	.	.	.	.	.	.	.	.	.	st.
Catillaria chalybeia	o.	.	.	o.	.	.	.	.	.	–	–	o.	.	.	.	.	st.
Icmadophila ericetorum	.	.	.	.	.	.	.	.	.	o.	o.	.	.	.	.	.	
Candelariella vitellina	o.	o.	o.	o.	o.	f.	–	o.	o.	o.	o.	o.	o.	.	f.	.	st.
Physcia hispida	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	f.	.	t.
Buellia myriocarpa	o.	o.	o.	o.	o.	o.	–	.	.	o.	o.	o.	o.	o.	o.	.	st., t.
Rhizocarpon geographicum	.	.	o.	o.	o.	f.	o.	.	o.	f.	f.	f.	.	.	.	.	st.
R. petraeum	o.	o.	o.	o.	o.	o.	–	.	.	o.	–	o.	.	.	.	.	st.
R. confervoides	f.	f.	f.	f.	o.	f.	f.	f.	–	f.	f.	f.	o.	.	f.	.	st.
Bacidia umbrina	o.	o.	.	o.	.	.	.	.	.	o.	–	.	.	.	.	–	st.
Bilimbia sabuletorum	o.	o.	o.	o.	o.	o.	–	o.	o.	o.	o.	o.	o.	.	o.	.	
B. lignaria	o.	.	o.	.	o.	.	.	–	.	o.	o.	o.	.	.	–	.	
B. melaena	.	o.	.	o.	.	–	.	.	.	o.	f.	o.	.	.	.	.	
Haematomma coccineum	.	.	.	.	.	o.	.	.	.	o.	o.	o.	.	.	.	.	bo.
H. ventosum	.	.	.	.	.	o.	–	.	.	f.	f.	o.	.	.	.	.	bo.
Gyrophora polyphylla	.	.	.	.	.	o.	–	–	.	f.	f.	o.	.	.	.	.	bo.
G. cylindrica	.	.	.	.	.	o.	.	.	–	f.	f.	.	.	.	.	.	bo.
G. polyrrhiza	.	.	.	.	.	f.	.	.	.	o.	–	.	.	.	.	.	bo.
Cladina rangiferina	.	.	.	r.	.	o.	.	.	–	o.	o.	r.	.	.	.	.	
C. sylvatica	a.	a.	a.	a.	a.	a.	a.	a.	f.	a.	a.	a.	–	a.	a.	a.	x.
C. uncialis	f.	f.	f.	f.	.	a.	–	f.	o.	a.	a.	a.	.	a.	a.	.	
Cladonia foliacea	.	.	.	o.	o.	o.	.	.	.	–	–	.	.	.	.	.	
C. pyxidata var. chlorophaea with similar frequency	f.	f.	a.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	a.	f.	f.	
C. fimbriata	f.	f.	f.	f.	f.	f.	–	.	o.	f.	–	–	f.	f.	f.	–	
C. ochrochlora	o.	o.	o.	o.	o.	o.	.	.	.	o.	–	.	.	.	.	.	
C. pityrea	o.	o.	o.	o.	o.	o.	.	.	.	o.	–	o.	f.	.	f.	.	
C. degenerans	.	.	.	.	.	o.	.	o.	o.	o.	.	.	.	.	.	.	e.
C. subcervicornis	f.	f.	f.	f.	f.	a.	f.	f.	f.	f.	f.	f.	.	.	f.	.	
C. gracilis	r.	o.	o.	o.	r.	f.	.	.	–	f.	f.	f.	.	f.	–	.	
C. crispata	o.	o.	o.	o.	.	–	.	.	.	o.	–	.	.	f.	f.	.	i.
C. furcata	f.	f.	f.	f.	f.	f.	f.	f.	o.	f.	f.	f.	f.	f.	f.	–	u.
C. rangiformis	o.	o.	f.	o.	f.	o.	f.	o.	o.	f.	f.	f.	o.	o.	f.	–	g.
C. subsquamosa	.	r.	r.	o.	.	r.	–	.	.	o.	–	o.	.	.	.	.	
C. squamosa	o.	o.	.	f.	.	f.	o.	.	o.	o.	o.	.	.	o.	.	–	sh.
C. caespiticia	.	r.	.	.	r.	r.	.	.	–	–	–	.	.	.	o.	.	
C. coccifera	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	f.	–	
C. bellidiflora	.	.	.	.	.	–	.	.	.	o.	o.	.	.	.	.	.	
C. macilenta	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	.	–	f.	–	t.b.
C. flabelliformis	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	.	f.	–	.	
C. bacillaris	.	.	r.	.	.	–	.	.	o.	.	–	.	.	o.	.		
C. floerkeana	f.	f.	f.	a.	f.	a.	.	f.	f.	f.	f.	f.	f.	f.	f.	f.	v.
Pycnothelia papillaria	.	.	.	.	.	–	.	.	.	–	–	.	.	o.	.	.	
Baeomyces rufus	f.	f.	o.	f.	o.	o.	.	o.	o.	f.	f.	f.	.	.	o.	–	b.s.
B. roseus	o.	o.	o.	f.	.	o.	.	.	.	o.	o.	o.	.	.	o.	.	b.s.
Stereocaulon condensatum	.	.	.	.	.	o.	.	.	–	o.	o.	o.	.	.	.	.	
S. coralloides	.	.	.	r.	.	f.	–	.	.	f.	f.	.	.	.	.	.	st.
S. denudatum	.	.	.	o.	.	f.	.	.	.	f.	f.	.	.	.	.	.	st.
Crocynia lanuginosa	.	.	r.	.	o.	o.	.	.	.	o.	o.	.	.	.	.	.	b., ro.
Peltigera canina	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	o.	g.
P. rufescens	f.	f.	f.	f.	f.	f.	.	f.	o.	f.	f.	f.	o.	.	.	.	

	Upland heaths of Somerset					Heather moors							Wet heaths				Notes
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	
P. polydactyla	o.	o.	o.	o.	o.	f.	o.	o.	–	f.	f.	o.	o.	.	o.	.	g.b.
Peltidea aphthosa	.	.	.	.	.	–	–	.	–	o.	o.	r.	.	.	.	.	st.
Nephromium parile	.	.	.	.	.	o.	–	.	–	–	o.	.	.	.	.	.	m.r.
Leptogium sinuatum	o.	o.	o.	o.	f.	o.	o.	.	–	o.	o.	o.	.	.	.	.	s.c.
L. lacerum	o.	o.	f.	o.	f.	f.	f.	.	–	o.	o.	.	–	.	o.	–	or
L. microscopicum	o.	.	.	o.	o.	o.	.	.	–	o.	–	.	.	.	.	.	sh.
Ephebe lanata	.	.	.	o.	.	f.	.	.	.	o.	f.	.	.	.	.	.	d.r.
Ephebeia hispidula	.	.	.	.	.	o.	.	.	.	o.	o.	.	.	.	.	.	d.r.
Polychidium muscicolum	.	.	.	.	.	o.	–	.	.	o.	o.	.	.	.	.	.	
Stenocybe bryophila	.	.	.	.	.	r.	.	.	.	o.	.	.	.	.	.	.	y.
Coniocybe furfuracea	r.	r.	r.	r.	.	r.	.	–	r.	o.	o.	o.	.	.	o.	.	sh.
Sphaerophorus globosus	.	.	.	o.	.	f.	.	o.	r.	f.	f.	.	.	.	.	.	bo.
S. melanocarpus	.	.	.	.	.	r.	.	.	.	o.	o.	.	.	.	.	.	bo.
S. fragilis	.	.	.	.	.	o.	.	.	r.	o.	o.	.	.	.	.	.	bo.
Verrucaria maculiformis	o.	o.	o.	o.	o.	o.	.	.	.	l.f.	.	.	.	.	.	.	st.
V. mutabilis	.	.	.	o.	.	o.	.	.	.	.	.	.	.	.	.	.	st.
Microglaena nuda	o.	.	.	.	.	.	.	.	.	.	r.	r.	.	.	.	.	st.
M. breadalbanensis	.	.	.	.	.	.	.	.	.	.	r.	r.	.	.	.	.	st.
Porina chlorotica	o.	.	o.	o.	o.	o.	o.	.	r.	o.	r.	o.	.	.	.	.	st.
Coriscium viride	.	.	r.	.	.	o.	.	.	r.	o.	o.	.	.	.	–	.	
Botrydina vulgaris	f.	f.	f.	f.	f.	f.	f.	–	o.	f.	f.	f.	a.	f.	.	.	

UPLAND MOORS.

In *Types of British Vegetation* the upland moors of the Pennines are taken as examples, but in some respects they are not typical of such moors. The Southern Pennines are much affected by the smoke from the neighbouring industrial districts. The portion of the Pennines between Huddersfield and Stalybridge is the most floristically barren moorland in the British Isles. Within a few miles from the watershed of the range over 100 factory chimneys can be counted from one position and, unless the consumption of smoke can be made economically valuable, the stigma of barrenness will remain. Jefferies' account of Molinietum (**14**), Woodhead's general survey of the district (**35**), and the papers by Moss (**23** *a*, *c*), show the barrenness of these moors (see also (**1**)). Sphagnetum is poorly represented, Scirpetum is almost absent, whilst Eriophoretum is unduly developed. *Empetrum* is sometimes dominant over large areas, replacing *Calluna vulgaris* or *Vaccinium myrtillus*. *Eriophorum* or *Empetrum* is often dominant over large areas and this dominance is often so complete that no other vascular plants occur. This exclusiveness may partly be due, at the present time, to these plants being less affected by smoke than those which are displaced. Bryophytes suffer similarly to the phanerogams. Those which are epiphytic rarely occur except at the extreme bases of trees, even the forms of *Hypnum cupressiforme*, so common on tree trunks in many districts, being confined to such situations. Lichens, which seem to be the group of plants most susceptible to smoke, are comparatively rare and are seldom found with apothecia. *Lecanora varia*, so common on trees in similar but less smoke-affected districts, sometimes occurs as a sooty yellow incrustation. Its thallus is scarcely recognisable and apothecia are rarely present. If present they are usually externally deformed and their internal characters are ill-defined. In a similar way the hills in South Wales

show the influence of the smoke from the industrial districts. The nearer one gets to these districts the floristic poverty becomes more pronounced, especially in regard to the corticicolous bryophytes and lichens. The influence of smoke is sometimes strikingly shown in the neighbourhood of a steep incline on some Highland railways. For example, near Tyndrum station a steep incline necessitates an increased consumption of fuel and a greater discharge of smoke. The bryophytes and lichens become much poorer in the portions over which the smoke is usually carried, in fact it would be possible to calculate the prevailing local currents of the atmosphere from a detailed investigation of the local distribution of these plants.

Sphagnetum.

This is poorly represented in the Southern Pennines and seems to have played an insignificant part in the peat formation of that region (**35**). There is some evidence that it was formerly more extensive since *Sphagnum* can occasionally be obtained in thin layers from peat cuttings, at a depth of 2–3 ft. In such situations it is often sufficiently well preserved for specific determination and the species is sometimes one which is rare or absent in the district at the present time. *S. imbricatum*, obtained from peat cuttings at 1700 ft. between Oldham and Penistone, is not known to survive in the district. *S. papillosum*, as well as one of the accompanying mosses (*Hylocomium loreum*), is now infrequent or rare in the locality where the two were obtained from peat by Woodhead (**35**).

Sphagnetum is better represented in Perthshire, North Wales and on the higher parts of Exmoor (1100–1600 ft.). The commonest species in the drier Sphagneta are usually members of the Cymbifolia and Acutifolia groups, especially *S. papillosum* in the former and *S. quinquefarium* in the latter group. In the wettest Sphagneta *S. cuspidatum* is often the dominant species and some members of the Subsecundum group may be frequent, though the species of this group are usually more abundant in situations where the water is in motion. Some relations of Sphagna to their habitats have been expressed in a previous paper (**32** *e*) and a consideration of these relations enable an ecologist to form probable estimates as to the *Sphagnum* group of a particular habitat. *S. squarrosum* and *S. recurvum* (including *S. amblyphyllum*) are the most abundant Sphagna in shady situations, though these two bog mosses are also frequent in unshaded habitats. It must be borne in mind that there is a certain amount of plasticity, both in the species and the habitat, so that species of normally different habitats may be found intermixed. In such a Sphagnetum any of the plants given in the following lists may be present:

Viola palustris	f.	D. anglica	o.
Ranunculus lenormandi	r.	Menyanthes trifoliata	f.
Caltha palustris	r.	Hydrocotyle vulgaris	f.
Hypericum elodes	f.	Oxycoccus palustris	f.
Drosera rotundifolia	f.	Vaccinium uliginosum	l.
D. longifolia	o.	Erica tetralix	f.

E. cinerea	r.	P. strictum	o.
Calluna vulgaris	o.	Dicranum bonjeani	o.
Valeriana dioica	r.	Aulacomnium palustre	a.
Anagallis tenella	f.	Bryum pseudotriquetrum	o.
Pinguicula vulgaris	o.	Philonotis fontana	o.
P. lusitanica	l.f.	Hypnum stramineum	f.
Narthecium ossifragum	f.	H. cuspidatum	f.
Potamogeton polygonifolius	o.	H. scorpioides	o.
Andromeda polifolia	r.	Drepanocladus exannulatus	o
Scheuchzeria palustris	l.	Cephalozia connivens	f.
Betula pubescens	f.	C. macrostachya	l.f.
B. alba	f.	C. bicuspidata	o.
Myrica gale	f.	Aneura pinguis	o.
Pinus sylvestris	f.	Calypogeia fissa	f.
Eriophorum angustifolium	f.	C. trichomanis	o.
E. vaginatum	r.	Gymnocolea inflata	f.
E. latifolium	f.	Lophozia floerkeana	o.
E. gracile	l.	L. ventricosa	o.
Rhynchospora alba	f.	Odontoschisma sphagni	f.
Eleocharis multicaulis	o.	Leptoscyphus anomalus	o.
Carex pulicaris	f.	Pleurozia purpurea	l.
C. dioica	r.	Scapania dentata	o.
C. limosa	l.	Anabaena laxa	–
C. echinata	f.	Cylindrocystis brebissoni	–
C. oederi	o.	Micrasterias crux-melittensis	–
C. lasiocarpa	l.	Xanthidium armatum	–
Juncus articulatus	f.	Galera hypnorum var. sphagnorum	–
J. bufonius	o.	Mycena vitrea	–
J. effusus	o.	M. juncicola	–
Orchis praetermissa	o.	Tubaria paludosa	–
Nardus stricta	o.	T. stagnina	–
Molinia coerulea	f.	Nolanea juncea	–
Polytrichum commune	a.	Mitrula phallioides	–

The cloudberry, crowberry, ling and bracken occasionally occur in Sphagnetum but they cannot be considered as typical members of the association. Katz (16) gives *Vaccinium myrtillus, V. vitis-idaea, Melampyrum pratense, Carex inflata* and *Ledum palustre* as occurring in the Sphagnum bogs of Russia. The latter would probably grow in our Sphagnum bogs if introduced, but the others are certainly not typical Sphagnetum plants with us.

It is more usual to find one particular group of *Sphagnum* dominating the whole or part of the Sphagnetum. Though various species may occur together there is often one species more abundant than the rest, and, not only does this become the dominant one but may even be exclusive of the others. Then the floristic composition, even in regard to the algae, is of a more definite character. In one particular area, half an acre in extent, on the Blackdowns of South Somerset, *S. girgensohnii* is almost the only *Sphagnum* present, *S. cymbifolium* being the only other species noticed. On the drier parts of moorland *S. papillosum, S. cymbifolium* and *S. quinquefarium* often occur in almost pure patches, though in such situations some other member of the Acutifolia group (often *S. fuscum* in the Scottish Highlands according to Wheldon) and *S. rigidum* are frequently members of the association. On the sides of unwooded dells (cloughs or combes) pure masses of *S. quinquefarium* may be found 20–50 yards above the stream. *S. plumulosum* and *S. rubellum*, the other common members of the Acutifolia group, are usually found in wetter places. *S. cuspidatum* is the most hydrophilous species and is

frequently associated with *Drepanocladus fluitans, D. exannulatus* or other member of that genus (or sub-genus of *Hypnum*), *Cephalozia fluitans* and lax-leaved or floating forms of *Gymnocolea inflata*. On Exmoor (Dunkery above 1600 ft.) a floating form of *Ranunculus lenormandi* is associated with it. Many of the bryophytes amongst the *Sphagnum* of wet places are characterised by their lengthened shoots (Fig. 3). This is, of course, more noticeable in such species as *Brachythecium purum, Fissidens adiantoides, Hypnum schreberi, Calypogeia fissa, C. trichomanis, Lophozia ventricosa* and *Aneura pinguis*, which are normally members of drier associations.

Katz (**16**) finds similar associates of *Sphagnum* in the Sphagneta of Central Russia though there are some differences. Two of the dominant Sphagna of the Cymbifolia group in the Russian bogs are *S. medium* and *S. subbicolor*. These are much less abundant with us, their places being taken by other members (*S. papillosum* and *S. cymbifolium*) of the same group. *S. balticum* is rare with us, whilst *S. dusenii* is absent. *Ledum palustre* and *Cassandra calyculata* are frequent in the Russian bogs but are absent from our flora except where the former has been naturalised. The prevalence of *Eriophorum vaginatum* is not shown to the same extent, the allied *E. angustifolium* and *E. latifolium* being usually and relatively much commoner with us than in the Russian Sphagneta. The rarity of such species as *Vaccinium uliginosum, Scheuchzeria palustris, Carex limosa, C. lasiocarpa, C. pauciflora* with us is reflected by their local distribution. The richness of *S. medium* in dependent hepatics is less noticeable with us, except perhaps in the Highlands of Scotland, where our Sphagneta become more like those described by Katz; in fact, the general statement may be made that the similarity to our Sphagneta gradually becomes greater as we ascend from Southern England to more northern regions.

Eriophoretum.

Eriophoretum is characteristic of the Pennines but in a typical condition is not present on Exmoor, though both *Eriophorum vaginatum* and *E. angustifolium* are frequent. *Empetrum nigrum* not infrequently becomes the dominant or sub-dominant plant as on Kinder Scout, the moors from Crowden to Huddersfield, etc., whilst *Rubus chamaemorus* is dominant on some parts of the Pennines, e.g. the watershed between Yorkshire and Cheshire. From Edale Cross to Kinder Scout the Crowberry and Cotton grass association begins at 1750 ft. and ascends to 2088 ft. (This includes part of the retrogressive Eriophoretum mentioned in (**30** *a*), p. 274.) On Pots and Pans (Saddleworth) it is on a gently sloping plateau about 1400 ft. When the two common *Eriophora* occur near each other, the wetter places are usually occupied by *E. angustifolium*. The Eriophoretum vaginati is characteristic of the Southern Pennines, whilst the wetter Eriophoretum angustifolii is much more frequent on the Somerset moorlands.

Eriophoretum vaginati.

Eriophorum vaginatum	d.	Drepanocladus fluitans	o.
Empetrum nigrum	s.d.	var. atlanticus	f.
Rubus chamaemorus	s.d.	D. exannulatus	o.
Vaccinium myrtillus	r.—a.	Hylocomium squarrosum	r.
V. vitis-idaea	o.	Aplozia crenulata	r.
Eriophorum angustifolium	r.	Alicularia scalaris	o.
Erica tetralix	r.—l.a.	Lophozia ventricosa	f.
Molinia coerulea	r.	L. floerkii	f.
Scirpus caespitosus	r.—l.a.	L. atlantica	r.
Carex curta	o.	L. bicrenata	r.
Agrostis tenuis	o.	Gymncolea inflata	f.
A. alba	o.	Sphenolobus minutus	o.
Juncus squarrosus	o.	Cephalozia bicuspidata	o.
J. effusus	o.	C. connivens	o.
Sphagnum recurvum	o.	Diplophyllum albicans	f.
S. cymbifolium	o.	Cephaloziella starkii	a.
S. papillosum	o.	Leptoscyphus taylori	o.
Polytrichum commune	o.	Calypogeia fissa	r.
var. minus	o.	C. trichomanis	f.
P. aloides	r.	Lepidozia reptans	f.
Tetraphis pellucida	a.	Cladonia coccifera	a.
Ceratodon purpureus	o.	C. floerkeana	o.
Campylopus flexuosus	a.	C. macilenta	o.
C. pyriformis	o.	C. pungens	o.
Dicranella heteromalla	a.	C. squamosa	r.
D. cervicornis	o.	Cetraria aculeata	o.
Dicranum scoparium	o.	var. hispida	f.
Rhacomitrium lanuginosum	o.	Hypogymnia physodes	o.
Webera nutans	s.d.	Biatora uliginosa	o.
Mnium hornum	o.	B. granulosa	f.
Plagiothecium elegans	o.		

Eriophoretum angustifolii.

Many of the cryptogams present in Eriophoretum vaginati are absent or rarer in the wetter Eriophoretum angustifolii. The following list gives the most characteristic species.

Sphagnum cymbifolium	Aulacomnium palustre	Leptoscyphus anomalus˙
S. acutifolium	Drepanocladus exannulatus	Cephalozia fluitans
S. plumulosum	D. fluitans	C. bicuspidata
S. recurvum	D. aduncus (usually lowland)	C. connivens
Polytrichum commune	D. revolvens	Odontischisma sphagni
Campylopus brevipilus	H. scorpioides	Lepidozia setacea
Webera nutans	Gymnocolea inflata	

Scirpetum caespitosi.

Scirpus caespitosus is often frequent on upland moors but seldom becomes the dominant member of an association. On Dunkery (a heather moor) it is frequent, whilst on West Exmoor (near Simonsbath) a Scirpetum caespitosi is formed. It occupies the flatter portions of a hill 1400–1500 ft. high, the slopes leading down to the Exe Valley being wetter and occupied by Sphagneta. On the more gradual slope to the Barle Valley it passes into heath and then to heathy grassland. For the greater portion of the year it is saturated with water.

Scirpus caespitosus	d.	Vaccinium myrtillus	a.
Potentilla erecta	o.	Calluna vulgaris (usually small)	o.
Polygala serpyllacea	o.	Erica tetralix	r.

E. cinerea	r.		S. quinquefarium	o.	
Luzula multiflora	o.		Campylopus flexuosus	a.	
forma congesta	o.		Hypnum cupressiforme var. ericetorum	a.	
Anthoxanthum odoratum	o.		Hylocomium squarrosum	o.	
Nardus stricta	a.		Cephalozia bicuspidata	a.	
Deschampsia flexuosa	a.		Cephaloziella starkii	f.	
Sphagnum cymbifolium *forma* congestum	o.		Calypogeia fissa *forma* aquatica	o.	

In this Exmoor Scirpetum *Drosera rotundifolia, Narthecium ossifragum, Eriophorum angustifolium, Empetrum nigrum, Rhacomitrium lanuginosum, Cladina sylvatica* are not actual members, but occur on its margins. Ericas are seldom found in this Scirpetum though abundant in the surrounding associations. Scirpetum is shown on the Scotch hills and is similarly poor in diversity and number of species.

Vaccinieta myrtilli.

The three facies of this association described in *Types of British Vegetation* (**30**) generally have cryptogams similar to those of heather moor, though there are indications that they differ in detail. Most of the plants given in lists *F–L* from the moorlands of Dartmoor, Denbigh, Cannock Chase, Pennines, Llanberis, Killin, and Brecon occur in them. Both on Exmoor and Dartmoor patches of bilberry and heather moor occur, though heath is more usual. The Quantocks, Blackdowns and other Somerset hills usually have a heath vegetation which can scarcely be described as that of a heather moor except near the summits. On these wind-swept areas some retrogression may occur and the association becomes more or less open. Retrogression of Vaccinietum often occurs and sometimes the ravages of a caterpillar are responsible, as in that which occurred about 1910 at Kinder Low in Derbyshire. The initial phases which might lead to such a retrogression were also noted at Bwlch Gwyn in Denbigh. The facies of Vaccinietum occurring on steep sandstone screes and slopes has many bryophytes not commonly found in the other two, since the piled up rocks give shade and preserve more humid conditions. *Plagiothecium elegans* is often very abundant, whilst *Fissidens adiantioides, Lophozia attenuata* and *L. floerkii* are often present. Where *Allosurus crispus* is abundant, *Grimmia montana* is a characteristic plant of the small stones and boulders. This is especially noticeable at an altitude of about 1500 ft. on the steep talus-covered slopes of Foel Goch near Llanberis, other cryptogamic associates which are abundant being *Rhacomitrium sudeticum, Cetraria aculeata* and *C. islandica*. A similar association occurs in other parts of North Wales as in Cwm Clogwyn and on Cader, in both cases at an altitude below 2000 ft. and on block screes. Leach (**20**) gives a list of the bryophytes of non-calcareous block screes in the Lake District. A more general list in which lichens are included is given below. On the screes at Clogwyn some volcanic ash is present, and the presence of some calcium carbonate is indicated by the presence of *Grimmia conferta, G. andraeoides, G. apocarpa, Seligeria recurvata, Gymnomitrium adustum* and other plants which are not included in the following list:

Andreaea petrophila
Catharinea undulata
Polytrichum alpinum
P. piliferum
P. formosum
P. gracile
Dicranum scoparium
D. fuscescens
D. starkii
Campylopus flexuosus
Dicranella heteromalla
Rhacomitrium lanuginosum
R. fasciculare
R. sudeticum
Ceratodon purpureus
Webera nutans
Barbula rubella
Oedipodium griffithianum l.
Grimmia montana
G. torquata
Anoectangium compactum
Mnium hornum
Eurhynchium myosuroides
E. praelongum
Brachythecium rutabulum

Plagiothecium elegans
P. denticulatum
Hypnum cupressiforme
H. schreberi
Hylocomium loreum
H. squarrosum
H. splendens
Gymnomitrium crenulatum
Plagiochila asplenioides
Bazzania trilobata
Lepidozia pinnata l.
Alicularia scalaris
Lophozia attenuata
L. floerkii
Scapania gracilis
Diplophyllum albicans
Anastrepta orcadensis
Cetraria aculeata
C. islandica
Parmelia saxatilis
P. laevigata
Hypogymnia physodes
Squamaria gelida
Lecanora polytropa
L. intricata

Lecanora badia
Psora demissa
Lecidea contigua
L. sorediza
L. albocoerulescens
L. crustulata
L. dicksonii
L. kochiana
Haematomma ventosum
Rhizocarpon oederi
R. geographicum
R. confervoides
Bilimbia sabuletorum
B. melaena
Baeomyces roseus
Stereocaulon corallioides
S. denudatum
Cladonia furcata
C. gracilis
C. squamosa
C. verticillata
Cladina sylvatica
C. uncialis
Sphaerophorus globosus
Gyrophora cylindrica

Some of the bryophytes, and nearly all the lichens, given in the preceding list, cannot be considered as typical shade chomophytes since they occur on the exposed surfaces of the rock or ground. This is especially true for *P. piliferum*, and species of *Lecanora*, *Lecidea*, *Rhizocarpon* and *Gyrophora*. *Diplophyllum albicans* is ubiquitous, elongated pale green lax forms occurring in the shaded portions, whilst on the exposed parts the plants become very much shorter, darker in colour and with the leaves closely packed.

In a previous article (**32** *f*, p. 18) I have noted the chomophytic bryophytes of alpine block screes, especially for those at about 3000 ft. on Ben Lawers. Some calcium carbonate from weathered calcareous schist is present in this locality, and a few plants (*Hypnum molluscum, H. procerrimum, Brachythecium glareosum, B. plicatum, Mnium orthorrhynchum, Trichostomum tortuosum*) indicating this, are shown in the list. When these are omitted the list becomes fairly representative of alpine non-calcareous block screes. *Rhacomitrium ramulosum* should be included, as this is very abundant in a corrie on Ben Doran.

Kobendza and Motyka (**19**) give an interesting account of screes of fallen blocks which are comparable with ours. These fallen blocks are on the Lysa Gora hills of Poland and at a height below 600 m. On allowance being made for local conditions the flora is similar to that found on our screes, except that liverworts act more frequently as pioneers and that a few alpine lichens, which are considered as probable relics, are present. The authors trace the succession from a hepatic vegetation (chiefly species of *Lophozia*) to Polytrichetum. This then develops into Sphagnetum or Cladonietum according to the amount of moisture present between the blocks. (A review appears in This JOURN. **20**, No. 1, 1932, p. 218.)

HEATHER MOOR.

Callunetum vulgaris.

The floristic composition of seven of these is shown in the general list (*F–L*). In Somerset true heather moor is shown on Exmoor, but the list *D* of plants from this locality refers to the portions which are better regarded as upland heath. The following plants are characteristic of the Callunetum vulgaris of Exmoor.

The heathland of the Mendip is given as an upland heath, but it has some claim to be considered as a true heather moor. Its characteristic plants are given in list *E*.

Callunetum vulgaris of Exmoor.

Calluna vulgaris	a.	Leucobryum glaucum	o.
Polygala serpyllacea	o.	Mnium hornum	o.
Ulex gallii	o.	Plagiothecium elegans (a. in crevices)	f.
Potentilla erecta	f.	P. undulatum (rare plant of typical	o.
Galium saxatile	f.	heather moor)	
Vaccinium myrtillus	a.	Brachythecium purum	a.
Erica cinerea	a.	Hypnum cupressiforme (type)	r.
E. tetralix	o.	var. ericetorum	s.d.
Melampyrum pratense	o.	H. schreberi	a.
Digitalis purpurea	r.	Hylocomium splendens	o.
Rumex acetosella	o.	H. squarrosum	o.
Empetrum nigrum	o.	H. loreum	o.
Juncus squarrosus	f.	Aliecularia scalaris	f.
Luzula multiflora	o.	Aplozia crenulata (bare banks)	f.
L. pilosa	f.	Lophozia ventricosa	f.
Scirpus caespitosus	f.	L. bicrenata	r.
Eriophorum vaginatum	r.	L. floerkii	r.
Carex diversicolor	o.	Cephalozia bicuspidata	f.
C. binervis	o.	Cephaloziella starkii	f.
Agrostis setacea	f.	Gymnocolea inflata	f.
Deschampsia flexuosa	f.	Lepidozia reptans	o.
Molinia coerulea	o.	Ptilidium ciliare	o.
Festuca ovina	o.	Scapania curta	o.
Nardus stricta	o.	Lophocolea bidentata	o.
Pteris aquilina	r.—l.a.	L. cuspidata	f.
Blechnum spicant	o.	Calypogeia trichomanis	f.
Lastrea aristata	o.	C. fissa	o.
Polypodium vulgare	o.	Diplophyllum albicans	a.
Lycopodium clavatum	o.	Peltigera canina	o.
L. selago	r.	P. rufescens	o.
Tetraphis pellucida	o.—a.	Hypogymnia physodes (on rocks,	o.
Polytrichum piliferum	f.	ground or ling)	
P. juniperinum	a.	Parmelia saxatilis (on rocks)	f.
P. formosum (shady places)	o.	P. omphalodes (on rocks)	o.
P. commune (wetter places)	o.	Platysma glaucum (usually on rocks)	o.
Dicranum scoparium	a.	Cladonia coccifera	a.
D. majus (shady places)	o.	forma cornucopoides	f.
Campylopus flexuosus	o.	C. floerkeana forma trachypoda	a.
C. pyriformis	f.	C. subcervicornis	f.
Ceratodon purpureus (a short form with	a.	C. pyxidata	f.
nerve slightly excurrent also occurs)		C. furcata	f.
Rhacomitrium lanuginosum	o.	C. macilenta	o.
R. canescens var. ericoides (chiefly on	o.	C. flabelliformis	o.
washed sand)		Cladina rangiferina	r.
Dicranella heteromalla	a.	C. sylvatica	a.
D. cerviculata	f.	forma pumila	o.
Webera nutans (much more robust	a.	C. uncialis	a.
when well shaded)		forma aduncu	o.

Baeomyces roseus	f.	B. uliginosa	a.
Cetraria aculeata	f.	Botrydina vulgaris	f.
Lecidea contigua (a. on stones)	a.	Zygnema ericetorum	f.—a.
Biatora granulosa	a.		

The following plants are rare or absent on Exmoor but they are characteristic of heather moors in the north:

Oligotrichum hercynicum	Sphenolobus minutus	C. amaurocraea
Polytrichum alpinum	Cephalozia connivens	Cladonia bellidiflora
Rhacomitrium heterostichum	Lepidozia setacea	C. degenerans
R. fasciculare	Alectoria chalybeiformis	Stereocaulon coralloides
Orthodontium heterocarpum	A. bicolor (rocks)	S. denudatum
Leptodontium flexifolium	Parmelia laevigata	S. condensatum
Hylocomium loreum	P. omphalodes (rocks)	Pannaria pezizoides
Lophozia alpestris	Cetraria islandica	Psoroma hypnorum
L. floerkii	Platysma glaucum	Massalongia carnosa
L. atlantica	Icmadophila ericetorum	Sphaerophorus globosus
L. attenuata	Cladina rangiferina	S. melanocarpus
L. barbata	C. alpestris	S. fragile

Where rocks occur *Lecanora badia, Lecidea kochiana, L. griseoatra, L. dicksonii, Rhizocarpon geographicum, Haematotomma coccineum, H. ventosum, Gyrophora polyphylla, G. cylindrica, G. polyrrhiza, Umbilicaria pustulata, Ephebe lanata* (moist) and *Polychidium muscicolum* are also frequent. Some of the plants included in the tabulated list may also become more frequent.

In wet places (see society of stagnant hollows, **30** *a*, p. 279) the following are present:

Eriophorum angustifolium (in wetter places than E. vaginatum and Narthecium ossifragum)	Aulacomnium palustre
	Dicranella squarrosa
Drosera rotundifolia	Philonotis fontana
Sphagnum cuspidatum and var. falcatum var. serrulatum (submerged)	Drepanocladus exannulatus
	D. fluitans
S. cymbifolium	D. revolvens
S. plumulosum	D. falcatus
Gymnocolea inflata *forma* natans (submerged)	Hypnum cuspidatum
Polytrichum commune	H. stellatum
	H. ochraceum

GRASS MOOR ASSOCIATION.

This is very common in Perthshire, Westmorland, Carnarvonshire and Merionethshire. In Somerset the hills are often cultivated right to their summits; true heather moors are found on Exmoor but heath is more abundant.

Molinietum coeruleae is the damper association and contains

Sphagnum cymbifolium var. congestum	Campylopus atrovirens
S. papillosum var. confertum	Hypnum fluitans
S. compactum	Cephalozia bicuspidata
S. quinquefarium	Calypogeia trichomanis
Aulacomnium palustre	Gymnocolea inflata
Bryum pseudotriquetrum	Alicularia scalaris
B. pallens	Scapania curta
Leucobryum glaucum	Diplophyllum albicans

Nardetum strictae has few bryophytes though the following occur:

Polytrichum gracile	–	Brachythecium rutabulum	–
P. piliferum	f.	Drepanocladus uncinatus	r.
P. juniperinum	–	Hypnum schreberi	–
Ceratodon purpureus	a.	H. cupressiforme var. ericetorum	a.
Dicranella heteromalla	f.	Hylocomium squarrosum	a.
Campylopus pyriformis	–	H. splendens	a.
Dicranum scoparium	f.	H. triquetrum	o.
Barbula convoluta	–	Alicularia scalaris	–
B. fallax	–	Lophozia ventricosa	–
Thuidium tamariscinum	–	Lophocolea bidentata	a.
Mnium hornum	–	L. cuspidata	a.
Plagiothecium denticulatum	–	Ptilidum ciliare	–
Eurhynchium swartzii	–	Diplophyllum albicans	–

Lichens are usually rare though Cladonias, especially *C. furcata*, are sometimes frequent. In Somerset Nardetum is little developed, occurring chiefly by the sides of moorland tracks, a common situation for this association in other counties.

<div align="center">

HEATH ASSOCIATION.

Callunetum arenosum.

</div>

This association occurs in Somerset on the Quantocks, Blackdowns, Brendons and parts of Exmoor. Most of the plants given in the list on p. 105, **30** *a*, are found on Somerset Calluneta. *Genista pilosa, Gentiana pneumonanthe, Juniperus communis, Schoenus nigricans* are absent, and *Campanula rotundifolia* very rarely occurs. The infrequency of the latter is very noticeable to an observer accustomed to northern heaths, in fact it is almost confined to calcareous districts in Somerset, though not necessarily to calcareous soil. In the general lists (*A–E*) the plants of five Somerset upland heaths are given. The Mendip heath (*E*) is included, though it has some claim to be classed as a heather moor. Their edaphic characters have been briefly noted on p. 285.

A more generalised account of the bryophytes and lichens of upland heath is given below. Chief vascular plants: *Calluna vulgaris* d., *Erica cinerea* f., *E. tetralix* (sometimes present in slightly damper places and mixed with *E. cinerea* but it is usually only found in moister parts), *Polygala serpyllacea* f., *Ulex gallii* (often attacked by *Cuscuta*, forming brown patches several square yards in size and visible 100 yards away) a., *Potentilla erecta* f., *Galium saxatile* f., *Veronica serpyllifolia* f., *Melampyrum pratense* f., *Vaccinium myrtillus* f., *Agrostis setacea* a., *Deschampsia flexuosa* a., *Pteris aquilina* l.a. *Rumex acetosella* is sometimes frequent whilst *Wahlenbergia hederacea* usually occurs in wetter places.

Where *Calluna* is dense very little grows (even mosses may be absent) besides *Cladina sylvatica*, its form *impexa* and *Hypogymnia physodes*. The latter may grow on the ground but is usually epiphytic, together with *Lecanora varia*, on ling stems. Where the *Calluna* is a little more open, *Hypnum cupressiforme* var. *ericetorum* is abundant and is accompanied by *Dicranum scoparium*,

Campylopus flexuosus, Webera nutans, Hylocomium splendens, Brachythecium purum. Any of these mosses may become the dominant one.

Hypnum cupressiforme var. *ericetorum* is the chief and almost the only moss where the bracken is dense. It is often the dominant moss with ling and gorse and may (like some species of *Drepanocladus*) possess many brown, long and branched rhizoids on the face of its leaf.

Brachythecium purum or *Hypnum schreberi* is often the dominant moss in damp portions where grasses are frequent. In rather moister portions with *Sphagnum*, both these species lose their characteristic pinnation or complanation and their branches become very long and exceedingly straggling.

Hylocomium squarrosum is very abundant in places where the typical heath vegetation is absent. On some heaths spruces have been planted; under these or near them a grass-like carpet of this moss occurs. Apart from these patches *H. squarrosum* is rather a member of grassy moor, siliceous grassland, or heathy pastures.

Webera nutans may be the most abundant moss when the ling is not dense, or when turfy patches occur, or other members of the Ericaceae (e.g. bilberry) become abundant.

Hylocomium splendens in more exposed places has its outer leaves almost without chlorophyll, their apices and upper portions being non-chlorophyllous. The branch leaves have more chloroplasts; in the upper portions they are in a few central rows of cells, and absent from the marginal rows.

Ceratodon purpureus is abundant when *Calluna* is small or less abundant. In some forms growing in dry places the leaves are more longly lanceolate.

Polytrichum commune (wet)	f.	Alicularia scalaris	f.
P. formosum (shaded)	a.	Lophozia ventricosa	o.
P. gracile	o.	Scapania compacta	o.
P. juniperinum	a.	S. gracilis	o.
P. piliferum	a.	Calypogeia trichomanis	f.
P. aloides (usually on path-sides)	f.	Cephalozia bicuspidata	f.
P. nanum	r.	Diplophyllum albicans	f.
Catharinea undulata	f.	Lepidozia reptans (especially shady)	f.
Ceratodon purpureus	a.	Peltigera canina	o.
Dicranella heteromalla	a.	Hypogymnia physodes (on stems of ling)	a.
Campylopus flexuosus	a.—l.d.		
Dicranum scoparium	a.	Parmelia saxatilis	f.
Rhacomitrum canescens var. ericoides (sand of drainage paths, etc.)	o.	Lecanora varia (on ling)	o.
		Cladina sylvatica	a.
Webera nutans	a.	forma impexa	a.
Bryum capillare	o.	C. rangiferina	r.
Aulacomnium palustre (damper)	f.	Cladonia pyxidata	f.
Mnium hornum	f.	C. pityrea	o.
Thuidium tamariscinum (shady)	f.	C. subcervicornis	f.
Brachythecium purum	a.—l.d.	C. foliacea (alcicornis)	o.
B. albicans	o.	C. coccifera	f.
Hypnum cupressiforme var. ericetorum	d.	C. macilenta	o.
H. schreberi	a.	C. floerkeana	r.
Hylocomium splendens	a.	forma trachypoda	f.
H. squarrosum	a.	C. furcata	f.
H. triquetrum (leaves sometimes slightly undulate)	o.	C. rangiformis	o.
		Baeomyces rufus	f.
Lophocolea bidentata	o.	B. roseus	o.
L. cuspidata	f.	Lecidea contigua (on stones)	a.

WET HEATH.

Bryophytic zonation.

The bryophytic zonation of a *Myrica-Molinia* heath has been previously described (**32** *d*) for a Somerset heath near Chard. This heath consists largely of *Molinia* tussocks with intervening water channels. Starting at the lowest level the zones of vegetation are: (1) *Potamogeton polygonifolius*, (2) *Aneura pinguis* and *Pellia epiphylla* OR *Hypnum scorpioides* OR *Sphagnum cymbifolium*, (3) *Aneura multifida*, (4) *Hypnum intermedium* OR *Sphagnum plumulosum*, (5) *Hypnum cuspidatum*, (6) *Brachythecium purum*, (7) *Hypnum cupressiforme* var. *ericetorum* (Figs. 1 and 2). A similar zonation has been
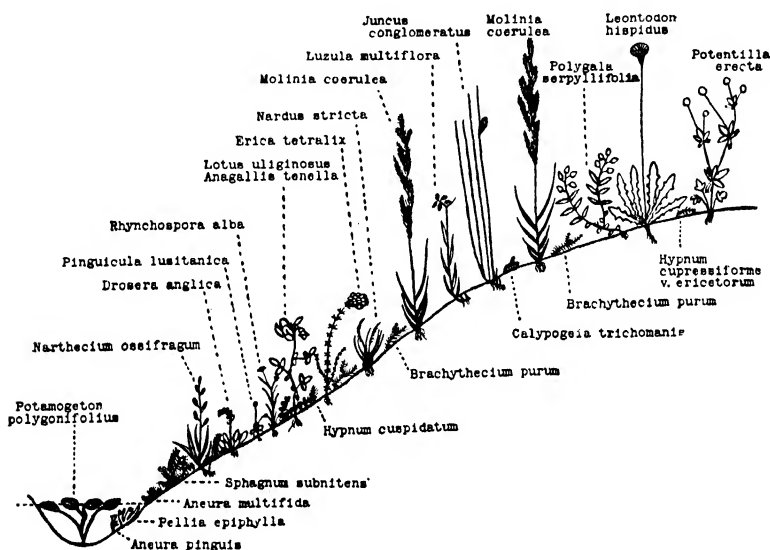
Fig. 1. Section through a water channel and a tussock, Chard Common. Scale 1 in 10.
The section passes through a zone of *Sphagnum plumulosum (subnitens)*.

noticed on many of the wet heaths of Somerset, though the zonation is usually less definite and some of the bryophytes may be replaced by plants with similar ecological characters. The inconstant zone of *Aneura multifida* at the water-level has been found to be of common occurrence and agrees with the author's observations in other parts of the country. As an example of a similar zonation, Widcombe moor on the Blackdown hills near Taunton, may be considered. This is a *Myrica-Molinia-Erica tetralix* heath and, like that on Chard Common, has its wettest portion at a higher level than the drier part. The drainage channels similarly contain *Potamogeton polygonifolius*, but the zonation is not so definite and some of the alternative zonation is not represented. (1) *P. polygonifolius*. Desmids are abundant. Two of the handsomest species, *Micrasterias cruxmelitensis* and *Xanthidium armatum*, occur in some of the bog pools.

(2) *Aneura pinguis* (a *Pellia*-like form) and *Pellia epiphylla*. No *Hypnum scorpioides* was seen and, as *Sphagnum inundatum* is more abundant than *S. cymbifolium*, the circulation of the water in the channels is probably quicker. (3) *Aneura multifida*. (4) *Sphagnum plumulosum* (*subnitens*) is dominant. *S. rubellum*, which also occurs on Chard Common, and *S. cymbifolium* are frequent. In these tufts of Sphagna *Odontoschisma sphagni* and *Hypnum stramineum* frequently occur. The facies of *Hypnum* (*Drepanocladus*) *intermedium* is not shown. (5) *Hypnum cuspidatum* occurs but this zone is not distinguishable from the fourth. *Veronica scutellata* and *Myosotis caespi-*
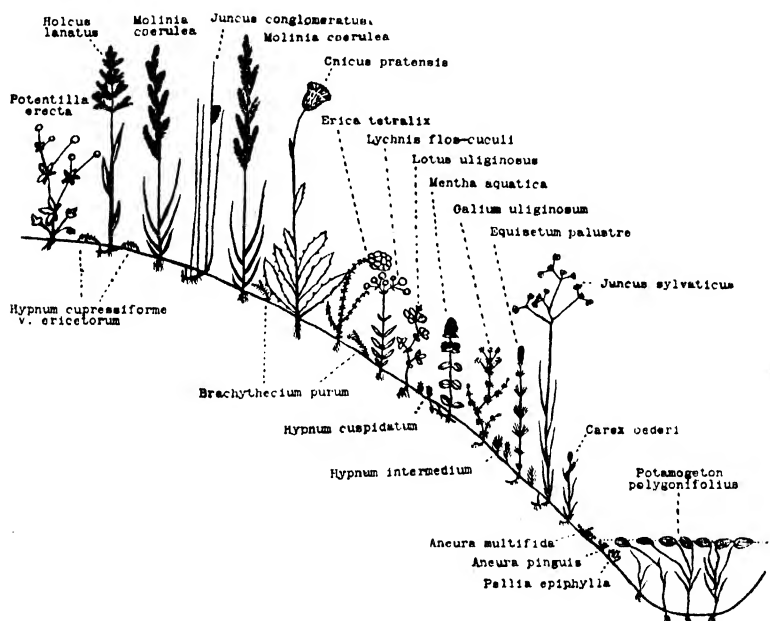
Fig. 2. Section through a wide water-channel and one of the highest tussocks, Chard Common. Scale 1 in 10. The section passes through a *Hypnum intermedium* zone.

tosa are present. (6) *Brachythecium purum*. When this moss is intermixed with *Sphagnum* its shoots are much less pinnate than usual, being sometimes almost unbranched. (7) *H. cupressiforme* var. *ericetorum*. In this and the preceding zone *Myosotis palustris, Carex diversicolor, Sphagnum quinquefarium, Amblystegium filicinum* and *Cladina sylvatica* occur. *Pedicularis sylvatica* and *Cladonia crispata* occur in the drier parts.

Hypericum elodes	f.	Narthecium ossifragum	f.
Drosera rotundifolia	a.	Juncus effusus	a.
Menyanthes trifoliata	a.	J. conglomeratus	f.
Oxycoccus palustris	f.	J. sylvaticus	f.
Anagallis tenella	a.	J. bulbosus	f.
Pinguicula lusitanica	f.	J. articulatus	a.
Hydrocotyle vulgaris	f.	Eriophorum angustifolium	f.

Eleocharis multicaulis	–	Polytrichum commune	f.
Carex oederi var. oedocarpa	f.	Dicranum bonjeani	o.
C. echinata	–	Aulacomnium palustre	a.
Rhynchospora alba	o.	Mnium affine var. elatum	o.
Sphagnum subnitens	a.	Bryum pseudotriquetrum	o.
S. acutifolium	o.	Hypnum cuspidatum	f.
S. rubellum	f.	H. stramineum	f.
S. inundatum	f.	H. stellatum	o.
S. recurvum	f.	Aneura pinguis *forma* pellioides	–
S. cymbifolium	a.	Calypogeia fissa	a.

Odontoschisma sphagni, and *Cephalozia connivens* were found in the wetter and boggier places. *Drosera anglica*, the hybrid *D. obovata*, *Eriophorum latifolium* and *E. gracile* are found on a neighbouring heath.

On some *Myrica-Erica tetralix* heaths the *Pellia* and *Aneura* zone is represented by other hepatics; at Hirynys near Harlech by *Pallavicinia lyellii* with *Cephalozia connivens*, *C. bicuspidata* and *Calypogeia fissa*; at Arthog near Barmouth by *Pallavicinia* with *Aneura latifrons*, *C. connivens* and *Lophozia incisa*.

Shapwick turf moor.

In the general list the constituents of four wet heaths (*M*-*P*) are given. Though there is a considerable agreement in regard to the bryophytic constituents these heaths are somewhat variable in character and are briefly described below. The area in Somerset known as the turf moor has been partly described and its phanerogams listed by Moss (**23** *b*) and Barker and Gibson (**2**). It is so peculiar in character and contains so many rare species that it well merits a more detailed investigation than has yet been done. Its soil consists of peat (sometimes more than 12 ft. thick) and alluvial deposits with some recent marine beds (Burtle beds) overlying Lower Lias, Rhoetic and Red Marl. It is almost flat, being only a few feet above sea-level, in fact at some places actually below; and in winter time is often a vast sheet of water, the season being often well advanced before its summer activity can be resumed. Natural waters are few or possibly absent, though many artificial canals have been cut for drainage, even the possibly primitive river channels having been straightened. Besides this drainage so much planting and turf-cutting have been done that little of the primitive heathland remains. In some places it is a *Myrica-Molinia* heath, in others *Calluna* becomes dominant. The *p*H value of the water varies, but is rarely acid enough for *Sphagnum* to develop, or rather *Sphagnum* seldom occurs to ensure acid conditions by the adsorption of the base from salts (**32** *c*). The fauna is also peculiar, and the moor is a happy hunting ground for entomologists. The common earthworm (*Lumbricus*) rarely occurs, rabbits are not numerous except on the flanks of the hills, but "clegs" are so abundant as to cause serious discomfort to the field worker. It seems to have been originally a vast swamp which, owing to artificial drainage, has become available for willow cultivation, turf exploitation and in the drier places, for some ordinary agricultural operations.

In the ditches or other wet places *Hypnum cuspidatum* is abundant. *H. polygamum*, *H. stellatum* and *Drepanocladus aduncus* are frequent, whilst *D. fluitans* and *D. exannulatus* are occasional. On the wet bases of banks *Cephalozia bicuspidata*, *Cephaloziella hampeana*, *Calypogeia trichomanis* and *Marchantia polymorpha* are frequent, the last two occasionally becoming truly aquatic and submerged in the water. In *Calypogeia* the leaves become more distant and decurrent so that the stem has a winged appearance (Fig. 3). In *Marchantia* the air chambers and pores are little developed and the plant can easily be mistaken for a *Pellia*.
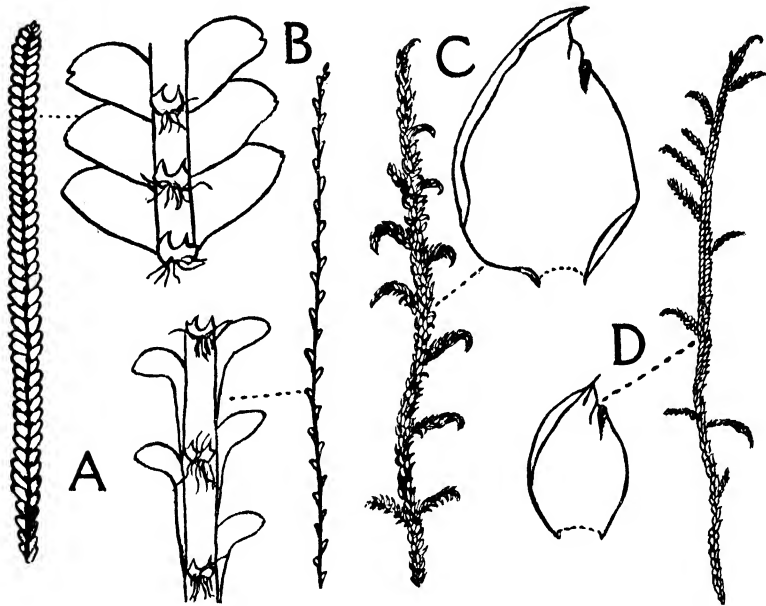
Fig. 3. A, B, *Calypogeia fissa* (L.) Raddi, two plants from the heath, Chard Common—A, a nearly typical plant though rather elongated; B, a slender form found in shadier and more aquatic situations. C, D, *Hypnum scorpioides* L.:—C, typical plant with a reddish colour, from zone (2); D, slender green form from zone (4), see p. 303. Plant in each case ×2; part of plant, or leaf, ×15.

On the vertical sides of cut peat both *Dicranella cerviculata* and *D. heteromalla* are frequent, often being associated with *Campylopus fragilis* and *Marchantia polymorpha*. On moist banks *Aulacomnium androgynum*, *Webera nutans*, *Bryum capillare*, *Mnium hornum*, *Dicranella cerviculata* and *Botrydina vulgaris* are abundant. The drier banks are usually somewhat damp except during exceptional drought. *Mnium hornum* is the dominant moss, *Polytrichum juniperum*, *Ceratodon purpureus* and *Dicranella heteromalla* are abundant, whilst *Tortula subulata* and *Campylopus fragilis* (often with *Barlaea cinnabarina* somewhat epiphytic on it) are frequent together with Cladonias such as forms of *C. pityrea* and *C. fimbriata*.

The Bagshot beds.

On the Tertiary beds of the Bagshot series extensive heaths, which are usually of a wet character, are found in Dorsetshire and Hampshire. They have a general likeness both in regard to topography and floristic constituents. Their surfaces are of a gentle undulating nature and few rock surfaces are exposed, except on the Studland heath, which is, however, similar in many portions and in most characters. The flora is not a rich one, especially in the parts where *Scirpus caespitosa* is a frequent constituent, but it is characteristic. *Ulex minor* is abundant, *Genista anglica* frequently occurs, and patches of *Gentiana pneumonanthe* give a vivid blue colour to many of the wet areas during the month of August. Species of *Sphagnum* are frequent in the wetter parts, *Campylopus brevipilus* is often commoner than *C. flexuosus*, *C. pyriformis*, *C. fragilis* or *C. atrovirens*, whilst *Dicranum* is represented not only by the common species, *D. scoparium* and *D. bonjeani*, but also by the rare *D. spurium*. *Hypnum cuspidatum* is abundant, *H. stramineum* and the rare *H. imponens* occur, but many of the heath-loving Hypna, such as *H. scorpioides*, *Drepanocladus fluitans*, *D. revolvens* and *D. intermedius* are rare or absent. *Webera nutans* and *Gymnocolea inflata* are, as usual, abundant and widely distributed, *Cephalozia fluitans* and *C. francisci* occasionally occur whilst *C. macrostachya* is often more frequent than the common *C. bicuspidata*. Amongst the lichens Cladonias, especially *Cladina sylvatica* and *C. uncialis*, are abundant, whilst *Pycnothelia papillaria* and *Biatora gelatinosa* are occasionally present.

Skipwith Common, Yorkshire.

Dry heath (Callunetum arenosum) is represented on this Common, but wet heath is more abundant. The alluvial deposits consist of sand and peat, the former being well shown on the drives and where it has been thrown out near rabbit burrows. The depth of the peat varies from a few inches to several feet and is thicker in the wetter portions. The ling varies very much in height and is often eaten down by rabbits, adventitious branches appearing above the nibbled parts. On the drier parts the ling (*Calluna*) is usually short, both *Erica cinerea* and *E. tetralix* are present, whilst *Nardus stricta* often forms a border 2 or 3 yards wide between the drive and the *Molinia* bordering the ditch. On the stems of *Calluna* and *Erica tetralix*, *Hypogymnia physodes* is occasionally present. In the same way *Lecanora varia*, which is almost the only lichen present on the birch and pine trunks, is frequently epiphytic. As on the Bagshot beds *Gentiana pneumonanthe* is a beautiful sight at the end of summer, its zenith being reached a little later than on the similar heaths of Dorset. Cladonias such as *C. sylvatica*, *C. crispata*, *C. furcata* and *C. gracilis* are abundant, *Cetraria islandica* and its variety *tenuifolia* are not uncommon, though the most frequent *Cetraria* is *C. aculeata*. In barer and drier patches

the form *hispida* of the latter often occupies areas from a few inches to several feet wide. Another lichen which is very noticeable is *Biatora granulosa* since it forms greenish orbicular patches of 1–3 in. diameter on damp peat.

Sphagnum occurs almost anywhere, in wet or moist or merely damp places. In the drier places it is in small patches or poorly developed and is often *S. compactum.* A congested form of *S. cymbifolium* is abundant in damp places amongst *Calluna* and *Erica tetralix.* The fibres of the cuticular cells are often weakly developed and the pores are larger than in the normal plant. *S. inundatum* is not uncommon where there is some slight movement of the water, whilst *S. crassifolium* and *S. cuspidatum* occur in ditches.

Juncetum societies are present around or in pools, *J. effusus* and *J. sylvaticus* being locally dominant whilst *J. bufonius* or *J. articulatus* are abundant in such moist places as Sphagnum bogs which are drying up. In pools *Potamogeton natans* or *P. polygonifolius,* accompanied by *Eleocharis palustris* and *Equisetum limosum,* are abundant, with Hypna present either in the water or at the edges. *Drepanocladus exannulatus, D. fluitans* and *D. lycopodioides* are usually in the water, *Hypnum giganteum* bordering it with *H. cuspidatum* forming a broad zone around.

Towards Escrick oak-birch heath occurs but much planting has gone on, many invaders are present and the vegetation is very variable. The bracken is locally dominant in or near the woods, in which such fungi as *Boletus edulis* are abundant, or occasionally on dryish heath. The bryophytes are similar to those of Callunetum arenosum with such plants as *Dicranum scoparium, Dicranella heteromalla, Leucobryum glaucum, Mnium hornum, Brachythecium purum, Hypnum cupressiforme* var. *ericetorum* and *Webera nutans* becoming locally abundant. The two last named are somewhat interchangeable, the *Webera* becoming more abundant in slightly damper places than the *Hypnum.* A few copses, sometimes birch, sometimes pine, sometimes mixed and with oak occur, and in the wetter places (especially in the pine woods) *Hydrocotyle vulgaris, Juncus effusus* and *J. sylvaticus* are abundant.

Betula pubescens	f.	D. fluitans var. arnellii (ditch)	o.
Pinus sylvestris (epiphytic lichens few)	f.	var. falcatum and var. gracile	o.
Sphagnum crassicladum (ditches)	–	D. intermedius	–
S. cuspidatum var. submersum (ditches)	–	D. exannulatus (in wet places)	a.
S. cymbifolium	a.	D. lycopodioides (pools)	–
var. congestum	a.	D. uncinatus	o.
S. compactum var. imbricatum (drier)	a.	D. sendtneri	o.
S. inundatum	f.	Hypnum cupressiforme var. ericetorum	d.
Webera nutans (in somewhat damp portions)	d.	(in drier portions)	
		H. cuspidatum	a.
Leucobryum glaucum	f.	H. imponens	o.
Campylopus atrovirens	f.	H. giganteum	–
Dicranum scoparium	f.	Alicularia scalaris	f.
D. bonjeani (amongst heather)	f	A. geoscypha (moist sandy places)	f.
Campylopus brevipilus (in moist places)	l.d.	Fossombronia dumortieri	o.
Polytrichum commune (moist places)	a.	Gymnocolea inflata var. laxa (in wet places)	a.
Aulacomnium palustre	a.		
Drepanocladus fluitans	f.	Lophocolea bidentata	o.

Cephaloziella starkii	a.	C. rangiformis	o.
C. hampeana var. pulchella	–	C. squamosa	o.
Cephalozia connivens	f.	C. furcata	f.
Lepidozia setacea	f.	C. crispata	f.
Leptoscyphus anomalus (in moist places)	o.	C. gracilis	f.
		C. uncialis *forma* adunca	a.
Hypogymnia physodes	o.	Cladina sylvatica	a.
Platysma glaucum	o.	Cetraria islandica	o.
Lecanora varia (on ling)	f.	C. aculeata	f.
Cladonia floerkeana *forma* trachypoda	f.	Biatora granulosa	f.
C. pyxidata	a.	B. uliginosa (on bare peat with Botrydina vulgaris)	f.
C. coccifera	f.		

Polytrichum juniperinum, *Dicranella heteromalla* and *Ceratodon purpureus* are frequent on edges of paths.

Delamere Forest.

This heathland is variable and in some parts is fairly well wooded, though the particular heath studied in the neighbourhood of Oakmere is less arboreal in character than many other parts. The underlying geological formation is of little importance, as the surface layers largely consist of alluvial deposits with varying thicknesses of peat. The bryophytes and lichens given in the general list are similar to those of Lindow Moss[1], the other Cheshire heath given on this page. There is also a general similarity of the floristic constituents with those of the heaths on the Bagshot Beds and with those of Skipwith Common. As examples of this similarity the occurrence of two rare hepatics may be noted. On all three heaths *Leptoscyphus anomalus* is associated with *Cephalozia connivens* and *Leucobryum glaucum*. *Cephalozia fluitans* occurs in wet places both at Delamere and on the Bagshot Beds. Many species of Sphagna occur in the wet places, and amongst other plants not mentioned in the general list the following were noted: *Catharinea crispa*, *Fissidens incurvus*, *Weisia mucronata*, *Tetraplodon mnioides*, *Lophozia excisa* and *Scapania irrigua*.

Lindow Moss, Cheshire.

Lindow Moss and the adjacent Lindow Common and Racecourse represent transition stages between Sphagnetum and Betuletum. The Moss is much moister than the Common and has frequent patches of *Sphagnum* in its moister or wetter places. It may be described as a Sphagno-Eriophoro-Callunetum. The peat is often several feet thick. The surrounding Common has peat a few inches to 2 ft. thick on a sandy subsoil, is fairly dry and now appears to be degenerating oak-birch heath. The flora is not a rich one and is certainly much poorer than it formerly was. The cryptogams are few though a more

---

[1] **Tansley (30 *b*)** calls wet moors "Mosses," which is a name often applied to them in Cheshire. On the Southern Pennines the term "Moss" is sometimes applied to upland moor in which *Eriophorum* is abundant or dominant.

intensive study would doubtless increase their number. As in many other Cheshire mosses the underlying geological formation is the New Red Sandstone, but as the surface layer is drift material, it has little effect on the flora. The different conditions of the Moss and Common give rise to a slightly different flora, which is often shown in a different frequency of a particular species rather than in its presence in one area and its absence in the other. In the following list the second frequency letter refers to the Moss.

Calluna vulgaris	d.d.	Deschampsia flexuosa	f.f.
Erica tetralix	o.a.	D. caespitosa	o.
Betula pubescens	a.o.	Juncus sylvaticus (wet places)	o.o.
Potentilla erecta	a.a.	J. effusus	o.
Galium saxatile	a.o.	J. conglomeratus	o.
Andromeda polifolia	l.a.	Eriophorum angustifolium (wet places)	o.o.
Oxycoccus quadripetalus	l.a.	E. vaginatum	o.o.
Pteris aquilina	l.d., l.a.	Equisetum limosum (wet places)	o.
Juncus squarrosus	o.a.	Sphagnum spp.	o.a.
Molinia coerulea	a.l.d.	S. cuspidatum var. falcatum	r.a.
Agrostis canina	a.l.d.	var. submersum (in ditches)	r.o.
Ulex europaeus	a.	S. recurvum var. amblyphyllum	r.a.
Viola ericetorum	o.o.	S. inundatum (pool sides)	r.a.
Polygala serpyllacea	o.o.	Polytrichum commune (moist spots)	o.a.
Crataegus monogyna	o.	Dicranella heteromalla (sides of paths)	a.a.
Pyrus aucuparia	o.	D. cerviculata (bare peat, peat cuttings)	o.a.
Prunus cerasus	o.	Webera nutans	d.d.
Drosera rotundifolia (in moist places)	a.o.	var. longiseta (in shady places)	o.o.
Rubus caesius	f.f.	Mnium hornum	o.
R. idaeus	f.f.	Funaria hygrometrica	o.
R. fruticosus	f.f.	Drepanocladus exannulatus	a.o.
Scabiosa succisa	f.o.	D. aduncus	o.
Hydrocotyle vulgaris (moist places)	o.o.	D. fluitans	a.o.
Lythrum salicaria (ditch sides)	o.o.	var. falcatum	a.a.
Epilobium angustifolium	o.o.	var. gracile	o.o.
E. hirsutum (wet places)	o.	Pellia epiphylla	o.o.
Galium mollugo	o.	Alicularia geoscypha	o.
Campanula rotundifolia	o.	Aplozia crenulata	o.
Solidago virgaurea	o.o.	Gymnocolea inflata	a.f.
Corydalis claviculata	o.o.	*forma* subaggregata	f.l.a.
Senecio jacobaea	o.	*forma* compacta (dryish ground)	f.l.a.
Crepis capillaris	f.	*forma* laxa (shaded)	f.f.
Betula alba	o.	Lophozia ventricosa	o.
Quercus robur	f.	Leptoscyphus anomalus	a.
Castanea sativa	o.	Calypogeia trichomanis	f.t.
Rumex acetosella	o.	Lepidozia setacea	a.
Alnus glutinosa	o.f.	Cephalozia connivens	a.
Salix caprea	f.f.	C. bicuspidata (moist places)	f.f.
S. cinerea	f.f.	Cladonia coccifera	o.a.
S. repens	f.f.	C. floerkeana *forma* trachypoda	a.
Potamogeton polygonifolius (wet places)	o.	C. pyxidata	o.
		Lecanora varia (on birches)	o.o.
Agrostis tenuis	o.o.	Biatora granulosa	a.a.
Glyceria fluitans (wet places)	o.	Agarics (few)	–
Nardus stricta	o.f.	Boletus edulis	o.

Sphagnum cuspidatum var. *falcatum* occurs in small patches with *Calluna* and *Erica tetralix*. *Funaria hygrometrica* was probably an invader; a few small cinders were found near it so that there had probably been a fire there. *Drepanocladus exannulatus* was on the edges of pools, ditch sides or in other moist or damp places: it was more typical on the edges of the pools; in the ditch bottoms it was drawn out, in the pools it was longer. *D. fluitans* var.

gracile usually had rhizoids at the tips of the leaves. *Alicularia geoscypha* was on damp peaty and sandy ground with *Calluna, Drosera, Juncus squarrosus, Nardus* and *Molinia* within a few inches of it. *Aplozia crenulata* was on moist sandy ground above a pool, *Cephalozia connivens* on cut surfaces near peat, above pools and on damp peat, whilst *Biatora granulosa* was abundant on either dryish or moist peat.

There is a general resemblance of the vegetation to that given for Delamere in the general list and also, though to a less extent, to the other three wet heaths. Most of the Lindow bryophytes and lichens are found in similar situations and with similar frequencies on all the other wet heaths. The occurrence of the rarer *Dicranella cerviculata, Alicularia geoscypha* and *Leptoscyphus anomalus* is especially noticeable.

Shapwick turf moor stands apart from the rest of the wet heaths in the paucity of *Sphagnum*, the bryophytes associated with it and in the rarity or absence of many foliose liverworts occurring in the other four heaths. In many respects it is like Wicken Fen, both in regard to fauna and flora, especially if the western and less acid portion of the turf moor is considered. A detailed and comparative analysis of the occurrence and frequencies of the vascular plants in the two areas is outside the scope of the present article, but the general likeness is very noticeable. All the mosses found at Wicken, with the possible exceptions of *Mnium affine* and *Hypnum elodes*, are found at Shapwick. The hepatics and lichens of Wicken Fen are so few that a comparison with the richer turf moor is of little value, though it may be mentioned that in the portions of the turf moor, where there is the closest resemblance to Wicken Fen, they are also few and embrace all the species noted in the fen.

SUMMARY.

The bryophytes and lichens of sixteen moorlands are given in a tabulated list. A few vascular plants are included in the list for the guidance of the phanerogamic botanist. These moorlands are considered as consisting of five dry upland heaths, seven heather moors of a damper nature and four wet heaths. The dry heaths are those of the Blackdowns, Brendons, Quantocks, Exmoor and Mendip in Somerset, the heather moors are situated in Dartmoor, Denbigh, Brecon, Snowdonia and Perthshire, whilst the four wet heaths are those of Delamere in Cheshire, Skipwith in Yorkshire, Shapwick in Somerset and of the Bagshot beds in Dorset. Brief accounts of these moorlands are given and some comparisons are made. Two other wet heaths are also described. Widcombe Moor in Somerset is given as an example of the bryophytic zonation described in a previous paper. Lindow Moss is compared with Delamere, the other Cheshire heath given in the tabulated list. Shapwick turf moor is variable, but in its less acid portions has some resemblance to Wicken Fen. The bryophytes and lichens of Sphagnetum, Eriophoretum, Vaccinietum and

Callunetum are noted in more detail. Those of Sphagnetum vary in accordance with the dominating *Sphagnum* group or species. In Vaccinietum the crypto-gamic plants of rock screes are specially dealt with.

The influence of a smoky atmosphere is evident from the examination of the bryophytes and lichens, especially the latter, of an industrial district.

Some modifications of bryophytes in accordance with habitat are dealt with.

REFERENCES.

(1) **Adamson, R. S.** "On the relationships of some Associations of the Southern Pennines." This JOURN. **6**, No. 2, 1918.

(2) **Barker, M. M.** and **Gibson, C. M.** "Studies of the Somerset turf moors." This JOURN. **10**, No. 2, 1922.

(3 *a*) **British Bryological Society.** *A Census Catalogue of British Mosses*, 1926.

(3 *b*) **British Bryological Society.** *A Census Catalogue of British Hepatics*, 1930.

(4) **Crampton, C. B.** and **Macgregor, M.** "The plant ecology of Ben Armine." *Scot. Geog. Journ.* **29**, 1913. Review, This JOURN. **1**, No. 3, 1913.

(5) **Darbishire, O. V.** "Some remarks on the ecology of lichens." This JOURN. **2**, No. 2, 1914.

(6 *a*) **Du Rietz, G. E.** *Zur Methodologischen Grundlage der Modernen Pflanzensoziologie.* Wien, 1921.

(6 *b*) **Du Rietz, G. E.** *Zur Kenntniss der Flechtenreichen in Sudnorwegen.* Upsala, 1925.

(6 *c*) **Du Rietz, G. E.** *Götlandische Vegetationsstudien.* Upsala, 1925.

(7 *a*) **Elgee, F.** *The Moorlands of North-eastern Yorkshire.* London, 1912.

(7 *b*) **Elgee, F.** "The vegetation of the Eastern Moorlands of Yorkshire." This JOURN. **2**, No. 1, 1914.

(8) **Evans, E. P.** "Warburton moss." This JOURN. **16**, No. 2, 1928.

(9) **Farrow, E. P.** "On the ecology of Breckland." This JOURN. **3**-**13**, 1915-25.

(10) **Frey, E.** *Die Vegetationsverhältnisse der Grimselgegend.* Bern, 1922.

(11 *a*) **Fritsch, F. E.** "The heath association of Hindhead Common." This JOURN. **15**, No. 2, 1927.

(11 *b*) **Fritsch, F. E.** and **Parker, W. M.** "The heath association on Hindhead Common." *New Phytol.* **12**, Nos. 4 and 5, 1913.

(11 *c*) **Fritsch, F. E.** and **Salisbury, E. J.** "Further observations on the heath association on Hindhead Common." *New Phytol.* **14**, 1915.

(12 *a*) **Godwin, H.** "The 'Sedge' and 'Litter' of Wicken Fen." This JOURN. **17**, No. 1, 1929.

(12 *b*) **Godwin, H.** and **Tansley, A. G.** *The Vegetation of Wicken Fen.* Cambridge, 1929.

(13) **Hopkinson, J. W.** "The ecology of the Bunter Sandstone." This JOURN. **15**, No. 1, 1927.

(14 *a*) **Jefferies, T. A.** "Ecology of the purple heath grass." This JOURN. **3**, No. 2, 1915.

(14 *b*) **Jefferies, T. A.** "Vegetative anatomy of *Molinia coerulea.*" *New Phytol.* **15**, 1916.

(15) **Jeffreys, H.** "General distribution of the vegetation of four Durham coal-measure fells." This JOURN. **4** and **5**, 1916-17.

(16) **Katz, N. J.** "Sphagnum bogs of Central Russia." This JOURN. **14**, No. 2, 1926.

(17) **Keller, B. A.** "Distribution of vegetation on the Plains of European Russia." This JOURN. **15**, No. 2, 1927.

(18) **Kertland, M. P. H.** "The ecology of Divis." This JOURN. **16**, No. 2, 1928.

(19) **Kobendza, R.** and **Motyka, J.** "La Végétation des éboulis des Monts de Ste Croix." *Bull. Acad. Polonaise*, 1929.

(20) **Leach, W.** "Vegetation of some non-calcareous British screes." This JOURN. **18**, 1930.

(21) **Lewis, F. J.** "Vegetation of peat areas in Central Alberta." This JOURN. **14**-**17**, 1926-29.

(22) **Macvicar, S. M.** "Distribution of hepatics in Scotland." *Trans. Roy. Soc. Edinburgh*, 1910.

(23 *a*) **Moss, C. E.** "Peat moors of the Pennines." *Geog. Journ.* 1904.

(23 *b*) **Moss, C. E.** "Geographical distribution of vegetation in Somerset." *Roy. Geog. Soc.* 1907.

(23 *c*) **Moss, C. E.** *Vegetation of the Peak District.* Cambridge, 1913.

(24) **Rayner, M. C.** "The ecology of *Calluna vulgaris.*" *New Phytol.* **12**, 1913.

(25) **Richards, P. W. M.** "Ecological notes on the Bryophytes of Middlesex." This JOURN. **16**, No. 2, 1928.

(26) **Rübel, E. A.** "Heath and steppe, Macchia and Garigue." This JOURN. **2**, No. 4, 1914.

(27) **Seifriz, W.** "The altitudinal distribution of lichens and mosses on Mt Gedeh, Java." This JOURN. **12**, No. 2, 1924.

(28) **Smith, W. G.** "The distribution of *Nardus stricta* in relation to peat." This JOURN. **6**, No. 1, 1918.

(29) **Summerhayes, V. S., Cole, L. W., Williams, P. H.** and **Richards, O. W.** "Studies on the ecology of English heaths." This JOURN. **12–14**, 1924–6.

(30 *a*) **Tansley, A. G.** and others. *Types of British Vegetation*, 1911.

(30 *b*) **Tansley, A. G.** *Practical Plant Ecology*, 1923.

(31) **Thatcher, K. M.** "The effect of peat on transpiration and growth." This JOURN. **9**, 1921.

(32 *a*) **Watson, W.** "Distribution of bryophytes in the woodlands of Somerset." *New Phytol.* 1909.

(32 *b*) **Watson, W.** "Xerophytic adaptations of bryophytes in relation to habitat." *New Phytol.* 1914.

(32 *c*) **Watson, W.** "Mosses of Somerset." *Proc. Som. Arch. and Nat. Hist. Soc.* 1912.

(32 *d*) **Watson, W.** "A Somerset heath and its bryophytic zonation." *New Phytol.* 1915.

(32 *e*) **Watson, W.** "Sphagna, their habitats, adaptations and associates." *Ann. of Bot.* 1918.

(32 *f*) **Watson, W.** "Bryophytes and lichens of arctic-alpine vegetation." This JOURN. **13**, No. 1, 1925.

(32 *g*) **Watson, W.** "Bryophytes and lichens of fresh water." This JOURN. **7**, No. 1, 1919.

(32 *h*) **Watson, W.** "Bog-mosses of Somerset." *Proc. Som. Arch. and Nat. Hist. Soc.* 1915.

(32 *i*) **Watson, W.** "Hepatics of Somerset." *Proc. Som. Arch. and Nat. Hist. Soc.* 1920.

(32 *j*) **Watson, W.** "Lichens of Somerset." *Proc. Som. Arch. and Nat. Hist. Soc.* 1930.

(33) **West, W.** "Ecology of the Upper Driva Valley in the Dovrefjeld." *New Phytol.* 1910.

(34 *a*) **Wheldon, J. A.** "Social groups and adaptive characters in the Bryophyta." *Lancs. Naturalist*, 1911.

(34 *b*) **Wheldon, J. A.** "The lichens of Perthshire." *Journ. of Bot.* Supp. 1915.

(35) **Woodhead, T. W.** "History of vegetation of the Southern Pennines." This JOURN. **17**, No. 1, 1929.

CURRENT SYSTEMS OF THE NORTH ATLANTIC AND THE NORTH SEA[1]

By J. R. LUMBY.

Fisheries Laboratory, Lowestoft.

(With five Figures in the Text.)

RATHER than attempting to give the details of the currents in the different parts of the Ocean (see, for example, (1)[2]), the object of the present paper is to present in a general way the modern conceptions and underlying principles regarding the water circulation.

To anyone wishing to become broadly acquainted with the surface circulation of the waters in the North Atlantic there are available two sources of information. The more detailed one consists of the current charts published in the various countries primarily for the use of seamen. Such information is usually set out in the form of current roses, showing the velocity, direction and frequency of the currents observed in a definite area during certain periods of time. When one merely needs a generalised view of the circulation, this is perhaps somewhat unwieldy and complicated to deal with, and in consequence one probably goes to the alternative source, which is the ordinary geographical atlas or text-book.

Here the circulation represented usually consists of a large whirl formed in the south by the Equatorial Current, in the west by the Gulf Stream, in the north by the North Atlantic Current (called by various names), and closed in the east by the Canaries Current. In the middle is a motionless region which includes the Sargasso Sea. Then we have the cold water supplied from the north by the Labrador and East Greenland Currents, forming perhaps a second, smaller whirl south of Greenland.

Such attempts at a general picture of the current system are themselves constructed mainly on the basis of the navigational information, of the kind which is set out in detail in the charts prepared to assist seamen.

At sea, it is the usual practice to work out each noon the position of the ship, first, by "dead reckoning" from a knowledge of her course and speed and, second, by means of astronomical sights. The difference between the two positions, if any, is attributed to the set of the current. Obviously, there are many factors here which can introduce error into the estimation of the current. For example, the ship is influenced by wind as well as current, and another factor is the accuracy with which the helmsman maintains the course. Moreover, the weaker and more transient the current is, the greater will be the effect of these errors on the estimation of it. If the current is a strong

one, always setting much in the same direction, then the data from the different ships will tend to agree, and our information regarding these regions will become so much the more reliable. Undoubtedly, however, these detailed charts serve their purpose well enough, which is to supply navigational information to seamen.

The data derived from ships can be supplemented also by information about the movements of derelicts, floating plants, drift bottles and flotsam in general. The combination of all this material is not such a straightforward and simple task as it might appear. A frequently quoted instance of the movement of a derelict will emphasise this (see (2)). In June, 1892, a schooner was cut in two at a spot roughly 260 miles easterly from New York. The after part floated high in the water and went northwards, while the fore part, which was awash, went towards the south-west.

What I wish to suggest, then, is that there are reasonable grounds for thinking that the generalised charts to be found in geographical text-books and atlases may not give a view of the circulation which it would be safe to use, for example, as an argument in a discussion on the causes underlying oceanic water movements; nor could it be used to furnish a satisfactory answer to the question: "Is it possible that a body put into the sea at one chosen point could reach another chosen point?"

Here it should be pointed out that there are two distinct ways of regarding water movements. We can either take, as it were, a snapshot and represent the motion at any moment by stream-lines, these stream-lines being curves, the tangent to which at any point represents the direction of motion at that point. Or we can follow a particle as it moves during a period of time and draw its path. The two pictures which we should obtain are the same only if the stream-lines are stationary; that is, if the currents themselves do not change from time to time. And, indeed, there is good reason to think that the North Atlantic circulation does change periodically with the seasons, and it probably changes aperiodically also. This distinction is important in finding an answer to such a question as the one I have put above. Nevertheless, in what follows these variations will have to be disregarded; broadly speaking, they are not very important in the present instance.

In presenting the modern conceptions of the oceanic circulation, it should, of course, be remarked that these views are not yet finally established, but there is no doubt that they are helping us to a better appreciation of the general state of affairs.

The ocean waters are in movement as a result of the presence of internal differences in structure along the meridians both in the atmosphere and in the hydrosphere. If we make a simplifying assumption that there were no land to interrupt and disturb the full development of these features, then, it has been shown, the surface water would move in belts round the earth roughly parallel to the lines of latitude.

On either side of the equator there would be west-going streams. Polarwards of these the flow would be eastwards, while in the polar regions themselves there would again be west-going streams. At the equator there would be a dynamically impelled east-going counter-current.

Now, not only along the meridians is the structure of the ocean not homogeneous, but in the vertical direction also, and in subtropical and tropical regions the water is divided into two more or less sharply defined layers.
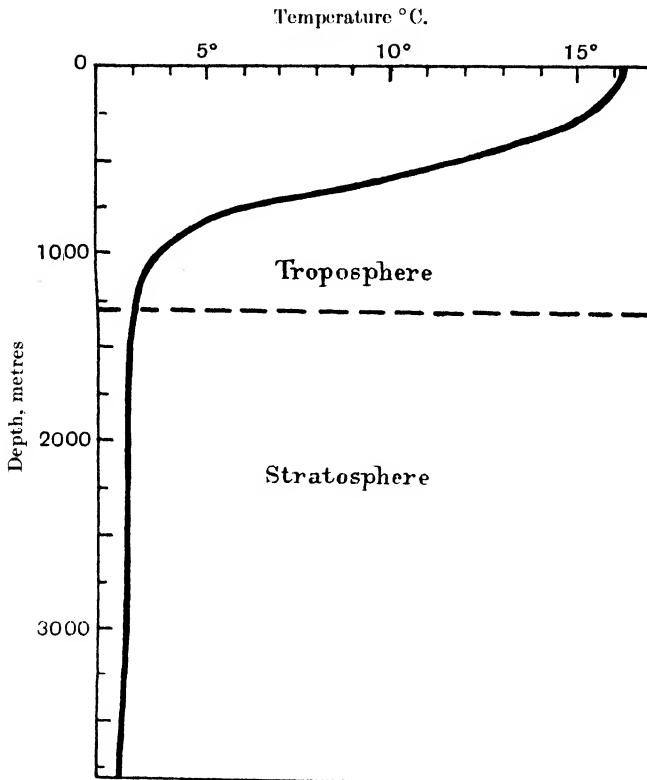
Fig. 1. Typical vertical temperature distribution in the ocean (after Defant (3) by kind permission). The lower boundary of the troposphere should be at about 600 m. instead of 1300 m. See Defant, "Dynamische Ozeanographie" (*Naturw Monogr. u. Lehrbücher*, **9**, 1929), Abb. 54, S. 137.

A shallow upper layer has a comparatively high temperature, and below this the temperature falls rapidly. Deeper still, the rate diminishes until the temperature becomes almost constant. According to a suggestion from the German oceanographers (3), the upper layer of high temperature in the oceans is termed the "troposphere" and the lower the "stratosphere," in analogy with meteorological terminology.

This layering of the sea, it may be noted in passing, is a feature often met with in oceanography. It may be of a permanent nature, as in the oceans, or

it may be merely temporary, but wherever it occurs it is never without considerable significance. In the northern, deeper parts of the North Sea, for example, two distinct layers are formed in spring and persist until the autumn. The extent to which the upper layer, some 40 metres thick, is effective in cutting off the lower layer from the atmosphere may be gauged from the fact that, while the temperature of the upper layer may become about 15° C., the bottom layer seldom has a temperature higher than 7° C., so long as the "thermocline" is in existence. In the course of the summer, the oxygen content of the lower water layer is frequently reduced to about half its saturation value. As far as the shallower seas (and lakes) are concerned, the terms "epithalassa" and "hypothalassa" are frequently used for the upper and under layers respectively.

The shallow oceanic troposphere, in immediate contact with the atmosphere, is the chief seat of the disturbances giving rise to the water movements, and the most active oceanic circulation is confined to this layer. In consequence of this sharp layering there is no appreciable transference of water in the vertical direction from the stratosphere to the troposphere. The troposphere does not, however, extend completely to the poles. In the polar regions it is the stratosphere which comes in contact with the atmosphere, and the lines which divide stratosphere from troposphere on the surface are termed the "polar fronts." The fronts are clearly recognisable in the surface temperature distribution by the crowding together of the isotherms. In consequence of this disposition of the stratosphere, the circulation here is strongly developed meridionally, in contrast with the zonal development of the troposphere.

In the polar regions we can distinguish between two kinds of water. Near the polar front, the water is freshened by the considerable precipitation, but it is still relatively cold. This water sinks below the surface and flows towards the equator, constituting the so-called Intermediate Current. In the ice regions nearer the poles, where the precipitation is slight, a still heavier water is formed owing to the loss of heat, especially in the polar winter. This water also flows equatorwards; as it occupies the very bottom-most level, it is termed the Bottom Current. Between these two currents is a compensation flow, termed the Deep Current, which runs polarwards. This circulation would, of course, be symmetrical about the equator.

Though, as has already been said, the tropospheric circulation is mainly zonal, i.e. east and west, it also has meridional components which are not without significance. Water flows north and south from the equator to about lat. 25°; there it sinks and returns equatorwards above the dividing surface between troposphere and stratosphere. Its sinking points correspond to the boundaries between the equatorial west-going streams and the subtropical east-going flows. These boundaries are termed the subtropic convergences, and it is here that the tropospheric warm waters tend to accumulate. Polarwards of these there are smaller closed circulations between the convergence

regions and the polar fronts. Thus, in our hypothetical ocean, there is no transfer vertically from stratosphere to troposphere, and the old notion of water from the very bottom rising to the surface at the equator must undoubtedly be discarded.

Now as to the extent to which this conception of the circulation is upheld by the observations available, it should be remarked that there are scarcely any direct measurements of the current in the open ocean, and we have to rely on being able to distinguish the different kinds of water by their physical and chemical characteristics and to follow their distribution.
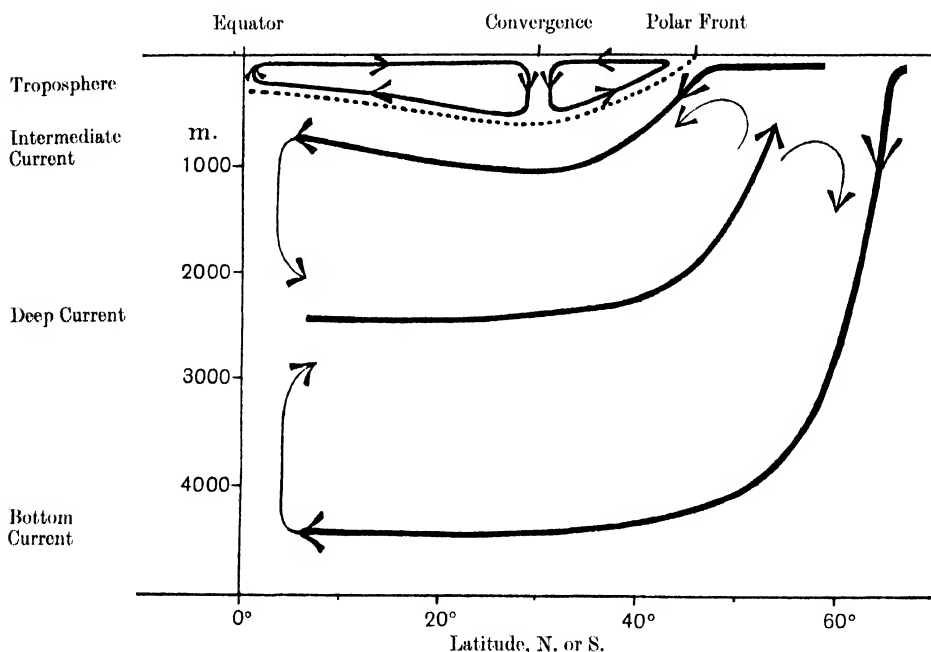
Fig. 2. Meridional circulation, symmetrical about the equator, in the hypothetical ocean (after Wüst (**11**) by kind permission).

Fig. 3 shows the vertical distribution of temperature and salinity in a roughly meridional section along one of the two troughs running through the Atlantic. One difference from our hypothetical ocean is immediately obvious, namely that the deep circulation is not symmetrical about the equator. Because this ocean is more open towards the south, the southern circulation is much better developed than the northern, which is barely recognisable. The salt and shallow troposphere is clearly to be seen in the uppermost layer, as well as the position of the polar fronts in about 40° S. and 50° N. Immediately below and coming from the surface in the Antarctic, the Intermediate Current is clearly indicated.

In about lat. 30° N. there is in the North Atlantic a transference of water from troposphere to stratosphere and the consequently salt Deep Current
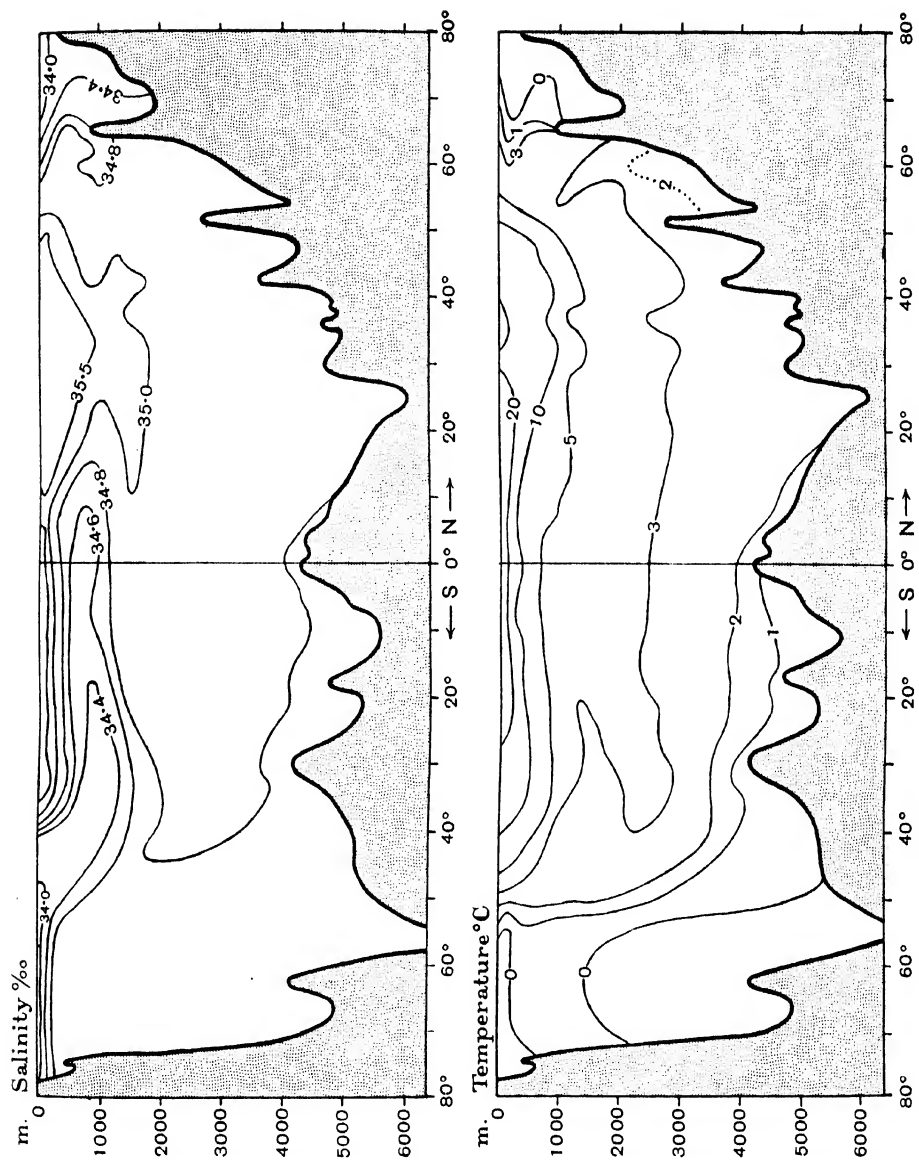
Fig. 3. Vertical distribution of Salinity and Temperature in the Western Atlantic (after Wüst (4) by kind permission).

returning to the south is easily distinguishable. Below this again is the equatorwards-streaming bottom water from the poles. This disposition of the currents is also recognisable in the distribution of temperature, which shows a marked inversion at about 1500 m. in lat. 30° S. In the convergence regions, especially the northern, the deepening of the isotherms clearly demonstrates the accumulation of warm water in these latitudes. That this deep circulation also has zonal components is evidenced by the fact that cold water from the Antarctic Intermediate Current (the current immediately below the troposphere) is found as a deeper layer in the Gulf Stream. It was formerly thought that this water must have been a southwards extension of the Labrador Current, but no connection with this current can be traced.

With these considerations in view, the German oceanographers took up afresh the study of the current information derived from ships. Fig. 4 represents the modern ideas of the surface circulation in the North Atlantic built up mainly in this way, though it is not based entirely on observations of this kind, because they are lacking in many regions. In such places information has been gathered from work done by research ships, and the chart combines these various investigations. Though it relates to the month of February, we may take it that a similar chart for other months would not differ in its essentials from this one.

There are two principal ways in which this chart contrasts with the earlier ones. First, the circulation is mainly zonal and, second, the central region of motionless water is replaced by the convergence region. Except for quite a narrow strip near the African coast the Equatorial Current has a mainly westerly trend. In comparison with it, the Gulf Stream, which formerly held the most important place in the picture, is relatively small and can be thought of as caused by the interruption of the zonal flow by the American continent. The east-going drift in about lat. 40° N. is also quite strongly marked, but it is diverted mainly north-eastwards by the European continent. The south-going stream off the southern European coasts is quite insignificant and cannot be considered as furnishing an adequate compensation for the transport westwards effected by the Equatorial Current. The compensation for this circulation must be sought in the depths.

There is, moreover, other evidence which supports this view of the strongly zonal development of the Atlantic currents.

If we plot the pressure contours of any surface in the sea relative to another surface, we can deduce the flow on the one surface relative to that of the other. If we can find a datum surface with no appreciable flow, then the actual currents can be deduced for the other surfaces. The isobars (the lines along which the pressure is the same) show the direction of the current, and the distance between them, corresponding to the gradient, is a measure of its velocity. An explanation may perhaps be offered for the fact that water flows along the isobars, and not across them, i.e. down the slope. There is

a law which states that if the water in the sea is to move with a uniform velocity and in an unchanging direction, it must be acted upon by a force
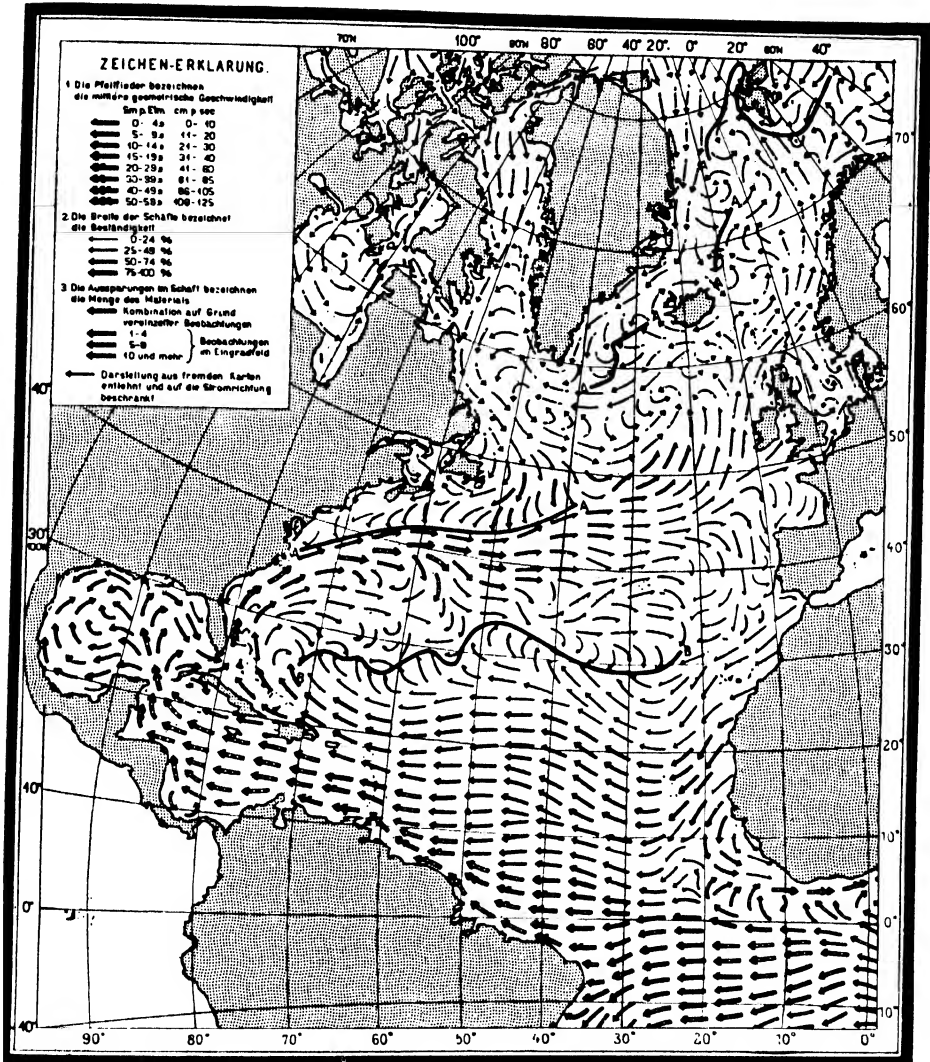
Fig. 4. Surface water circulation in the North Atlantic in February (from Wüst (**12**), after Meyer, by kind permission).

Explanation of signs. The arrow heads indicate the mean velocity and direction, the breadth of the shaft, the constancy, and the spaces in the shaft the number of data (the more spaces the fewer data). The narrow, broken arrows (mainly in the northern parts) refer to information from extraneous sources and indicate direction only.

which exactly balances the deflective effect of the earth's rotation. We may visualise the conditions in this way. Suppose a pressure field is represented

by isobars gradually changing from a low to a high pressure. Owing to the gradient the water begins to flow from the high pressure region towards the low. As soon, however, as it begins to move, the effect of the earth's rotation deflects it to the right. Though this effect is not a real force, in that it is incapable of setting up motion, we may regard it as one for the purpose of this explanation. This pseudo-force acts at right angles to the direction of motion of the water. It continues to deflect it until it is no longer running across the isobars but along them, and, at this moment, these two forces balance one another. Thus it is that the actuating force determines the velocity, not the acceleration, of currents in the sea, and when the force ceases to act, the motion ceases also.

Ekman (6) has published charts showing the dynamic topography of the surface in the North Atlantic relative to the 600 m. surface and to the 1000 m. surface. The contours indicate the direction of the current, and it is to be seen from them that the North Atlantic Current is a very well-developed current and not merely a rather vague drift, except in its south-eastern parts. Moreover, certain of its features point to the fact that it is a gradient, as well as a wind-driven, current. As to the eastern side, there is evidence that, apart perhaps from the most superficial layer, there is a considerable transport of water towards the north. During the winter season, water flows out most strongly from the Mediterranean on the bottom of Gibraltar Straits (it flows in at the surface most strongly during summer (7)), and this water, which is distinguishable from the true Atlantic water by its high salinity, is found spreading westwards and northwards right up into the Rockall Channel at a depth of some 1200 m. It may even be that it appears on occasions in the English Channel, but this is not certain.

There is one other feature of Ekman's charts to which attention may be directed, namely, the curious southerly bulge in the Gulf Stream, or Atlantic Current, southwards of the Newfoundland Banks. The peculiarity of the current in this region has been traced in the movements of icebergs by the International Ice Patrol, which service has added a great deal to our knowledge of the currents here. The Labrador Current strikes the flank of the Gulf Stream and, in the main, turns eastwards with it, not westwards, as was formerly held. The so-called "cold wall" off the North American coast has very little to do with the Labrador Current, but is an accumulation of coastal water from the rivers. This feature of the current system here is not very clearly represented on the chart (Fig. 4).

As regards this bending of the currents, one sometimes finds offered as an explanation the deflective force of the earth's rotation. For example, it is sometimes suggested that for this reason the Labrador Current should bend to the west along the North American coast and the Gulf Stream turns offshore. This view, however, is unsafe to put forward. As was shown earlier, the chief effect of the earth's rotation is to balance the force actuating the

current. If the force disappears, in a comparatively short time the current does too. The ocean currents do not go on running by their own inertia. If we could imagine a current doing so, it would indeed run in a roughly circular path, but the radius of the circle in the Gulf Stream region would be quite small, very much less, for example, than that of the curve in which the Gulf Stream actually flows.

North Sea. Naturally enough, the groundwork of our knowledge of the circulation in the North Sea is quite different from that concerning the Atlantic. In the first place, the chief water movements are due to oscillatory tidal currents, which more or less mask the residual drift, as it may be termed. Secondly, it covers a relatively very small area. Consequently we do not get the navigational information from ships such as we get from the Atlantic. Our knowledge in this case, therefore, rests on the results of special investigations, such as current measurements, drift-bottle experiments, observation of the salinity and temperature and so on. These systematic investigations are of comparatively recent date, having been begun not more than 40 or 50 years ago, and they have since been one of the objects of co-operative study by the International Council for the Exploration of the Sea.

The chief credit for pioneer work in this direction goes to the late Dr Fulton. By means of drift-bottle studies, he reached the conclusion that water flowed round the north of Scotland into the North Sea, turned south along its western side, then eastwards off the Yorkshire coast, northwards on the continental side, and so out. He also suggested the dependence of this circulation on the wind and its liability to change with the wind. The entry of water into the North Sea was later supported by salinity observations, which showed a tongue of salt water stretching inwards from the north and also north-east-wards from Dover Straits. The existence of this flow from the south was established by the Dutch oceanographers, and Carruthers (8) has recently done a great deal of work on this particular flow. He finds its mean value to be of the order of between 2 and 3 miles a day, but it may reach a strength of some $\frac{3}{4}$ of a knot; it is also subject to reversals of considerable magnitude.

Another feature of the circulation which was recognised fairly early in these investigations is that water flowed into the Skagerrack on the Danish side and out on the Norwegian side. Naturally enough, continued study has led to a more detailed knowledge of the flow everywhere in the North Sea, especially in its relation to the wind. For example, Carruthers has been able successfully to forecast the distribution of fish eggs in their drift away from the spawning ground. The most recent representations depart considerably, however, from the simplicity of the earliest conceptions. The expression of modern views is primarily due to Böhnecke (9), who based his work mainly on a study of salinity distribution. It may be said that considerable justification for those views has been found, as, for example, in the drift-bottle studies just published by Tait (10).
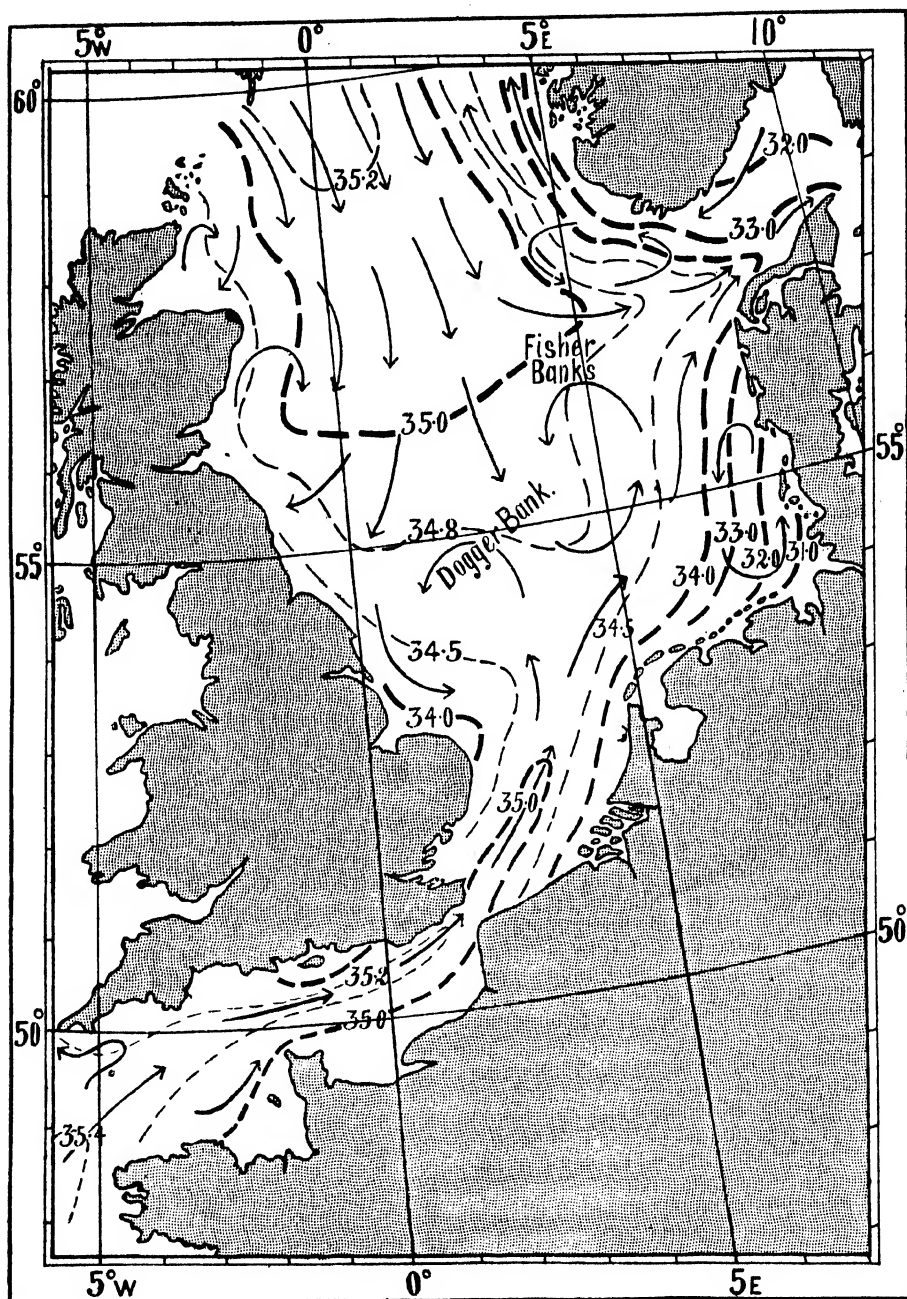
FIG. 5. The surface salinity (°/₀₀) distribution and water circulation typical of Winter
in the North Sea and English Channel. From *Fisheries Notice* No. 15, 1929 (Min. of
Agric. and Fish.). Reproduced by permission of the Controller of H.M. Stationery Office.

The chief differences between Fulton's and the modern views rest in the entry of the oceanic water north of the Shetlands and in the general complexity of the circulation. On entering the North Sea the water flows mainly south-eastwards to the Dogger Bank, forming bay swirls on the Scottish coast. Just before reaching the Dogger Bank, the stream divides into three branches, one running south-westerly, another south-easterly and the third eastwards into the Skagerrack. Where these streams meet the flow from the English Channel and from the Skagerrack, swirls are formed, which seem to be fairly constant in position. Tait adds a swirl in the most northern part of the North Sea (not shown in Fig. 5), and Wendicke suggested the existence of a swirl in the German Bight. This is not in the direction of a bay swirl, and is held to be due to the frequent westerly and north-westerly winds. This circulation seems fairly constant in its general character, though it is undoubtedly subject to both periodic and aperiodic variations, connected with the wind and probably with the variations in the Atlantic Stream.

Fig. 5 shows the general surface circulation together with the salinity distribution in the North Sea, and the connection between them may be readily seen. The winter conditions are given in preference to the summer ones, which tend to be less well defined and to exhibit more variation between one year and another than the former.

REFERENCES.

This list of references is not intended as a documentation of the foregoing article, but rather as a rough guide to further information.

(1) **Barlow, E. W.** "Currents in the North Atlantic Ocean." *Marine Observer*, 4, 48, London, 1927.

(2) **Marmer, H. A.** *The Sea*, p. 249. New York and London, 1930.

(3) **Defant, A.** "Die systematische Erforschung des Weltmeeres." *Zeit. d. Gesell. f. Erdkunde*, Jubil.-Sonderb., Berlin, 1928.

(4) **Wüst, G.** "Der Ursprung der Atlantischen Tiefenwässer." *Zeit. d. Gesell. f. Erdkunde*, Jubil.-Sonderb., Berlin, 1928.

(5) **Meyer, H. F.** "Die Oberflächenströmungen des Atlantischen Ozeans im Februar." *Veröff. d. Inst. f. Meeresk.* N.F., A, 11, Berlin, 1923.

(6) **Ekman, V. W.** "A survey of some theoretical investigations on ocean currents." *Journal du Conseil Int.* 3, 3, Copenhague, 1928.

(7) **Schott, G.** "Die Wasserbewegungen im Gebiete der Gibraltarstrasse." *Journal du Conseil Int.* 3, 2, Copenhague, 1928.

(8) **Carruthers, J. N.** "The flow of water through the Straits of Dover, etc." *Min. of Agr. and Fish., Fish. Invest.* II, 11, No. 1, London, 1928.

(9) **Böhnecke, G.** "Salzgehalt und Strömungen der Nordsee." *Veröff. d. Inst. f. Meeresk.* N.F., A, 10, Berlin, 1922.

(10) **Tait, J. B.** "The surface water drift in the northern and middle areas of the North Sea and in the Faroe-Shetland Channel." *Fish., Scot., Sci. Invest.* Nos. II and IV, Edinburgh, 1930.

(11) **Wüst, G.** "Meridionale Schichtung und Tiefenzirkulation in den Westhälften der drei Ozeane." *Journal du Conseil Int.* 5, 1, Copenhague, 1930.

(12) **Wüst, G.** "Der Golfstrom." *Zeit. d. Gesell. f. Erdkunde*, Jahrg. 1930, Nr. 1/2, Berlin, 1930.

PHAEOCYSTIS AND HERRING SHOALS

By R. E. SAVAGE.

Fisheries Laboratory, Lowestoft.

(*With Plate XXI and eleven Figures in the Text.*)

I. INTRODUCTORY.

THE influence of *Phaeocystis* on herring migrations has already formed the subject of a report by the present writer (9) and Figs. 5, 6 and 7 are copied from that source.

In the section dealing with diatoms, use has been made of three figures (Figs. 8, 10 and 11) from a report, which is still in preparation, dealing with the distribution of *Rhizosolenia styliformis* and *Biddulphia sinensis* and their relation to the shoaling of herring. Prof. A. C. Hardy and Mr J. R. Lumby are collaborating with the present writer in this report which it is hoped will shortly be published. The provisional conclusions drawn from this work are the writer's and are not to be considered as final.

The writer gratefully acknowledges his indebtedness to the Controller of H.M. Stationery Office for permission to reproduce these figures as well as Figs. 2, 3, 4 and 9.

II. WEEDY WATER.

One of the most striking features of the plankton in the sea is the occurrence in the spring of each year of the well-known "vernal maximum" when diatoms and other unicellular organisms increase rapidly in numbers, frequently causing the water to become discoloured, and to acquire a pungent odour. A similar outburst takes place in autumn, but, except for a few individual species, the resulting maximum is not usually as large as in spring.

These small organisms at the time of their maximum adhere to the nets of fishermen who variously refer to water containing them as "Dutchman's baccy juice," "stinking water," "weedy water," etc. Herring fishermen are most familiar with this phenomenon, and have learned to associate it with poor catches.

The principal cause of this weedy water in the southern North Sea is undoubtedly the colonial flagellate *Phaeocystis* which has both a spring and an autumn maximum, but certain diatoms also produce a similar effect, notably *Chaetoceras* spp. in spring; and *Rhizosolenia alata*, *R. styliformis* and *Biddulphia sinensis* in autumn. Diatoms, however, do not cause the nets to become as slimy as does *Phaeocystis*.

Phaeocystis pouchetii (Hariot) Lagerheim (Fig. 1) is a minute flagellate, $4-8\mu$ in diameter, which lives in colonies, the matrix of which is of a gelatinous nature. These colonies are visible to the naked eye, being about 1·0–2·0 mm. in diameter, and when abundant can easily be seen floating near the surface of the sea, giving the latter a muddy appearance.

We have some evidence in support of the view that herring are repelled by "baccy juice" when the latter is caused by *Phaeocystis*.

(a). Colony.   (b). Individual Cells   (c). Swarm Cell.
                                     of Colony.
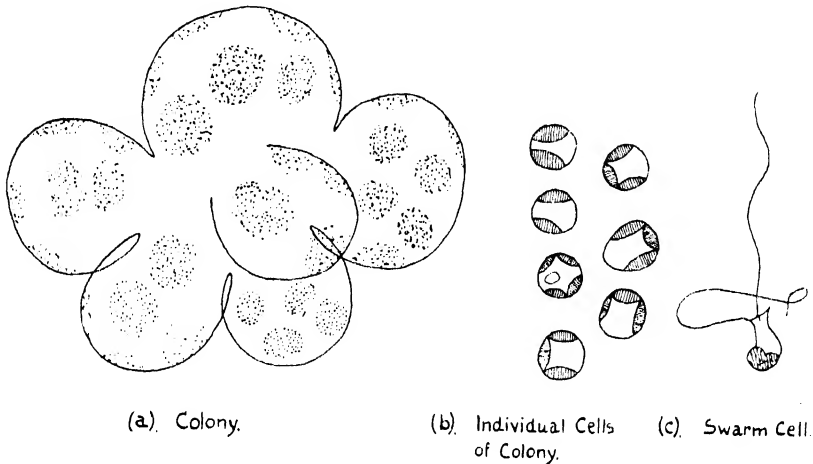
Fig. 1. *Phaeocystis pouchetii* (Hariot) Lagerheim. From Lemmermann after Lagerheim and Pouchet. ((a) × 40 diam., (b) and (c) × 1000 diam.)

III. The Migrations of the Herring.

Before considering this it would perhaps be as well briefly to indicate the main migrations of the herring in English waters, as far as we know them (Fig. 2).

We have first the feeding migrations, of which comparatively little is known. These probably take place over a wide area of the North Sea, the herring moving in shoals that are not large enough as a rule to enable a fishery to be prosecuted for their capture. Apart from the spring fishery off Lowestoft, when the herring have only just commenced to feed again after spawning, the feeding shoals are first encountered off the Northumberland coast about May. From May until August and September the stock is constantly being renewed by new recruits in the coastal waters from Northumberland to Yorkshire, although they are not usually found off the latter coast until August and September. The whole of this area is a rich feeding ground during these months, its local plankton being constantly reinforced by an influx of plankton in the Atlantic water from the north. (The herring is a plankton feeder.) South of about 54° N. lat. a great change comes over the plankton; between this position and about 53° N. lat. there is a kind of transition area
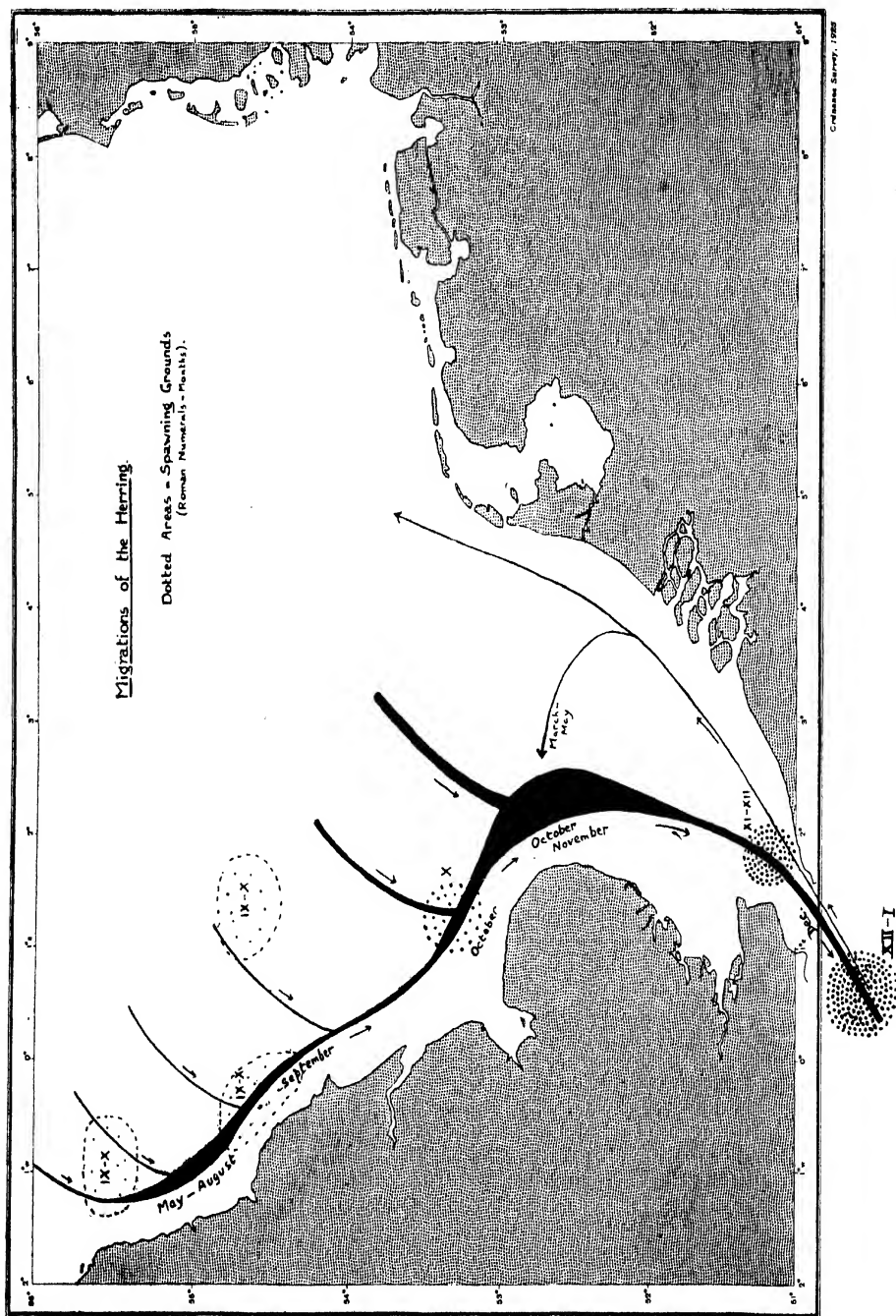
FIG. 2.   Diagrammatic representation of the migrations of the herring in the southern North Sea.   The thickness of the line is a rough indication of the quantities of herring.

between Atlantic water entering the North Sea from the north, and that entering from the south, and the zoo-plankton is usually very poor in quantity, i.e. as far as the western side of the North Sea is concerned. This area is very shallow, and consists of a series of elongated banks. A haul with a plankton net will bring up mainly sand, fragments of hydroids, polyzoa, and a few copepods, although occasionally we do find concentrations of diatoms here. This barren region also extends southwards along the Norfolk and Suffolk coasts. It will be seen therefore that the herring would receive little nourishment in this area, so that the feeding must all take place before the shoals pass into or through it.

About September the great spawning migration takes place, and the herring begin to arrive in East Anglian waters. The greatest part of these herring have done their feeding in grounds other than that off the north-east coast of England. Practically no feeding takes place during this spawning migration, mainly owing to the reduced appetite of the herring due to the onset of maturity, and to a lesser extent because there is practically no food for them; such as there is would be cleaned up by the first entrants. It is interesting to reflect that if the herring did not cease feeding during maturation there would probably never have been an autumn fishery off Lowestoft, as the herring would have gone elsewhere where food was plentiful.

An abundance of food might even be serious, as there is a possibility of the herring being unable properly to digest it at this time. We had some evidence of this in December of last year (1930). Some herring were landed at Lowestoft which had been caught near the Straits of Dover, and they were found to be in such poor condition that they were unsaleable. Our Inspector (Mr G. T. Atkinson) procured a few of these herring and brought them to me for examination. Their stomachs were tightly packed with decomposing food, which consisted of a mass of elongated strips of muscle and a multitude of paired eyes; obviously fish larvae and probably herring.

Some of the herring spawn in the East Anglian area, but the bulk of them do not do so until they later move farther south to the entrance of the English Channel, or in the western end of the Channel. (The principal spawning places are shown on the chart (Fig. 2) by dotted areas, the density of the dots being roughly proportional to the intensity of the spawning[1].)

After spawning the exhausted herring appear to drop out of the shoals, and in the early part of the year return to their feeding grounds in the North Sea and probably follow a course along the Belgian and Dutch coasts; it has been suggested that in their enfeebled condition they follow the line of least resistance and drift with the currents which would carry them in this direction. This is probably true, but there happens to be a good supply of food along this route, and the herring may merely be following this food track.

[1] For spawning grounds see **Hodgson (3)**.

IV. The distribution of plankton in spring and the effect of
Phaeocystis concentrations on the herring.

I would like now to sketch out what I think is the normal state of the
plankton in the Southern Bight in spring.

During the winter months the prevailing winds are generally from the
south-west, and it is highly probable that these winds cause the zoo-plankton
to drift to the eastern shores of the Southern Bight, for there we invariably
find copepods, etc., banked up as shown in Fig. 3 and Fig. 4 A. The hungry
herring coming through the Straits cannot miss this planktonic food, and can
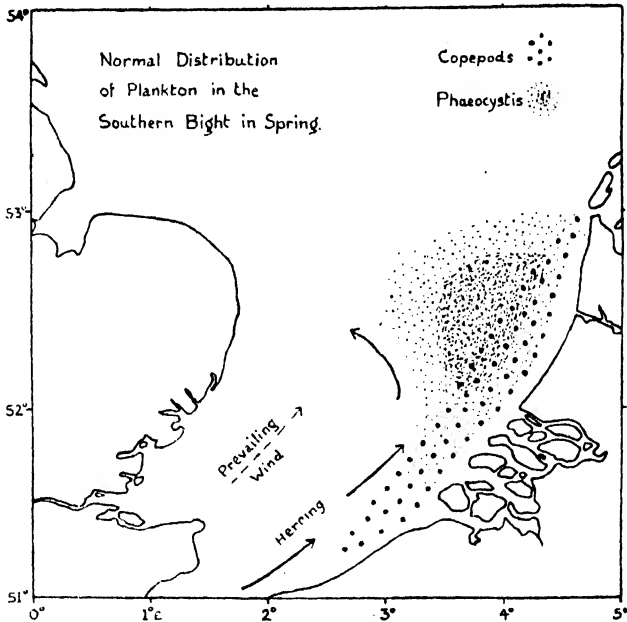
Fig. 3. Normal distribution of plankton in the
Southern Bight in spring.

continue their northerly migrations, somewhat recuperated, along this food
track. The later arrivals, however, may find their progress impeded by the
spring outburst of *Phaeocystis* which also seems normally to concentrate near
the Dutch coast. The herring do not appear to like this slimy and probably
unpalatable organism, and to avoid it must turn westwards, which brings
them off the Norfolk and Suffolk coasts. I believe that the Lowestoft spring
herring fishery probably owes its existence to the vernal maximum of *Phaeo-
cystis*. An early appearance of *Phaeocystis* in its normal locality would mean
a good spring fishery, as it would divert herring to our coasts at a time when
there were still large numbers of herring that had not yet migrated north-

wards; while a later maximum would mean a smaller fishery, as most of the herring would have passed by. This then is the normal condition as I see it.

At times, however, there is a more or less prolonged period when the wind blows from the east (Fig. 4 B), and under such circumstances the plankton tends to drift towards the English coast; the herring would follow their food, and larger catches would result; but if this onset from the east coincided with a *Phaeocystis* maximum, the latter would also tend to spread westwards, and this extension might be so great that the herring may even be turned

(A).   (B).

Key to Winds:

14·0 m.p.h.	3-9 Jan. 1921	S.B. = SWARTE BANK LIGHT-VESSEL.	17·6 m.p.h.	13-19 Dec. 1920
13·3 „	3-9 „ „	S.K. = SMITHS KNOLL LIGHT-VESSEL	12·2 „	6-12 „ „
11·0 „	4-8 „ „	F. = FELIXSTOWE	8·9 „	6-12 „ „
			15·4 „	13-19 „ „
			8·2 „	16-20 „ „
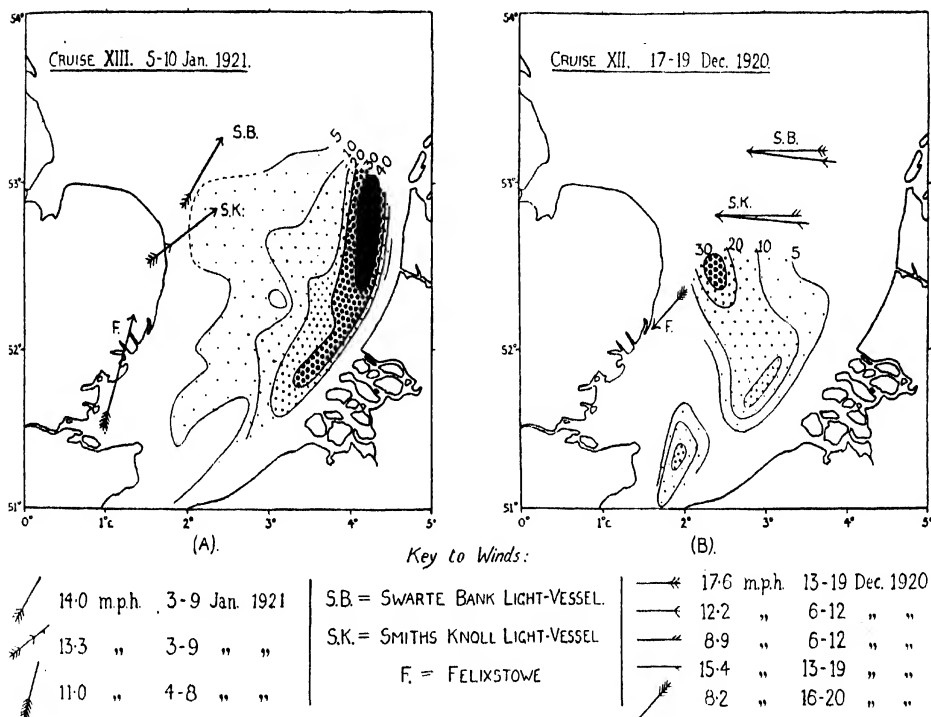
FIG. 4. The effect of wind from different quarters on the copepod *Pseudocalanus elongatus* (after Savage (**8**)). Wind data supplied by Dr J. N. Carruthers.

back and not reach our coast at all. The consequence would be a ruined fishery. We have some evidence in support of the latter condition, and also for the normal condition.

Fig. 5 shows the distribution of *Phaeocystis* in April, 1924, when it was in what I believe to be more or less its normal position. It will be seen that it is situated very near to the Dutch coast in such a position that it could prevent the herring from travelling near the coast and would divert them westwards as indicated by the arrows.

Fig. 6 shows the abnormal distribution of *Phaeocystis* in April, 1926. The concentration was very dense over the whole of the central part of the

Southern Bight, and probably acted as a very effective barrier to the migration of herring to our coast. The arrows show the assumed migrations of the herring, and it seems very probable that some of the herring were actually turned back.
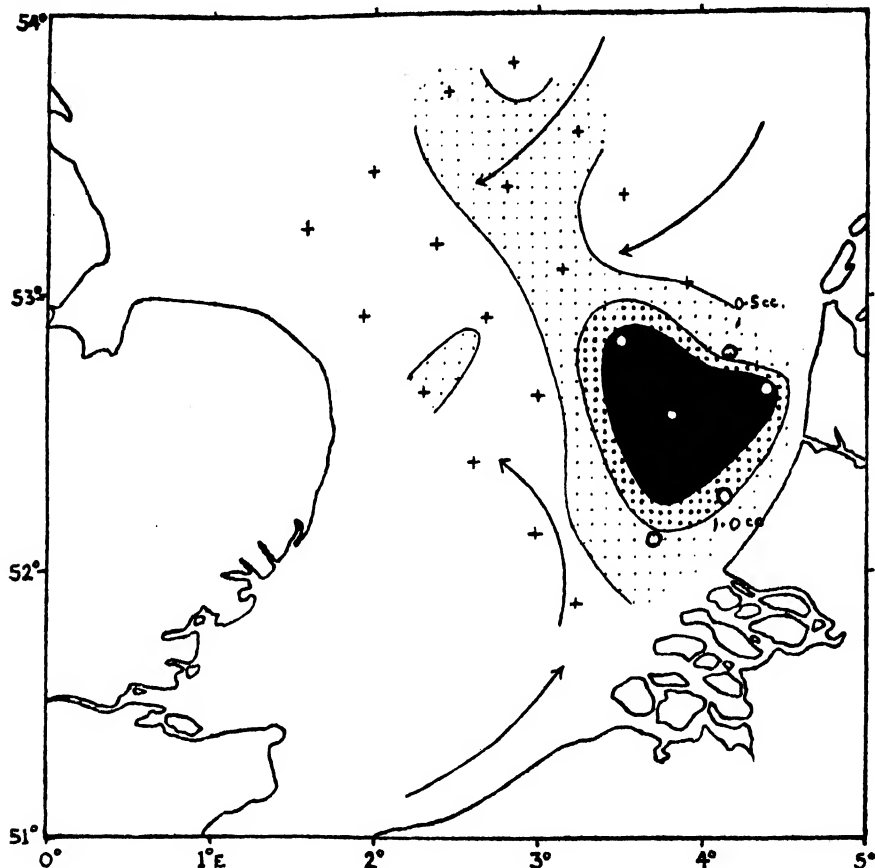
FIG. 5. The distribution of *Phaeocystis* during the period April 17th–24th, 1924. ○ = stations in *Phaeocystis* zone. + = stations where *Phaeocystis* was scarce or absent. The arrows indicate the assumed migrations of the herring. (Volumes per metre depth—Vertical hauls.)

The spring herring landings at Yarmouth and Lowestoft for these two years were:

	March cwt.	April cwt.	May cwt.	Total cwt.
1924	5968	**12971**	4426	23365
1926	677	**490**	751	1918

These figures support our theory as to the effect of *Phaeocystis* on herring migrations. The *Phaeocystis* maximum in both years was in April, and the landings for this month in 1924, when the flagellate was in its normal position, were over 26 times as large as in 1926 when it was in an abnormal position.

The spring fishery is of course only a comparatively small one, and the consequences of the adverse effect of *Phaeocystis* are not very serious. The summer fishery off the north-east coast is more important, but fortunately it takes place after *Phaeocystis* has reached its spring maximum, so that normally there is little to fear of any trouble from this source.
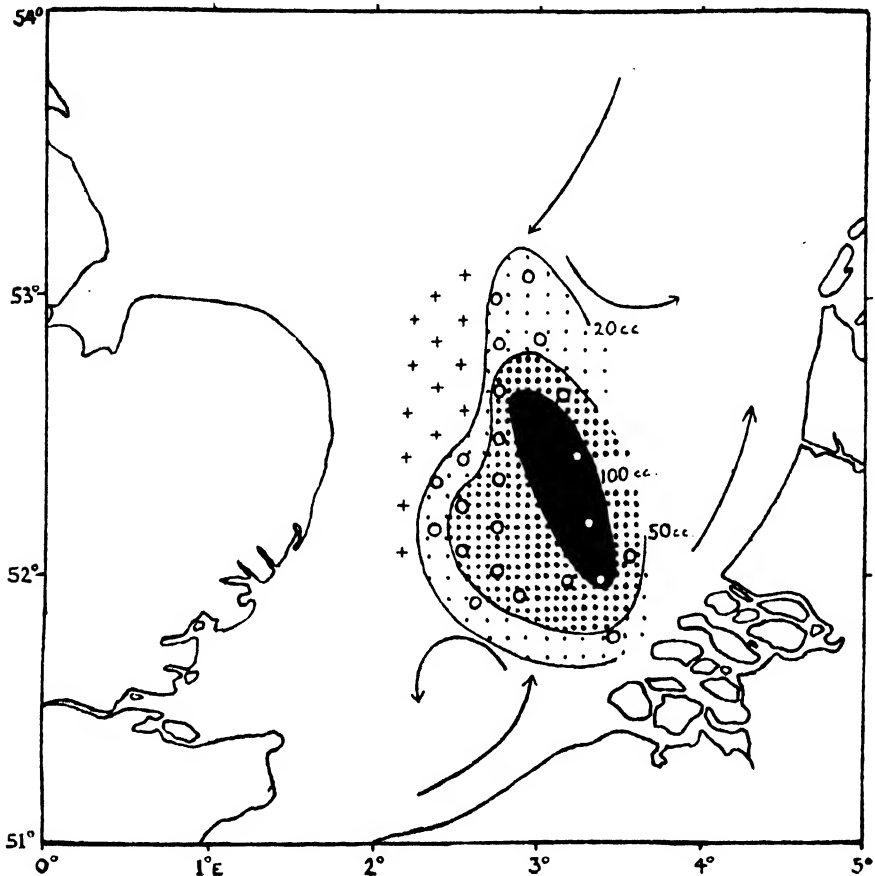
Fig. 6. The Distribution of *Phaeocystis* during the period April 8th–13th, 1926.
(Average volume per 10 minutes horizontal haul.)

V. *PHAEOCYSTIS* AND THE AUTUMN SHOALS.

An interference with the great autumn fishery off East Anglia, would, however, be a very serious matter, and it is a contingency that can occur, because as stated above, *Phaeocystis* has an autumnal maximum as well as one in spring. This actually happened in November of 1927 (Fig. 7). The herring suddenly deserted their usual shoaling grounds around Smith's Knoll Light-vessel, and were later located a considerable distance further east in a
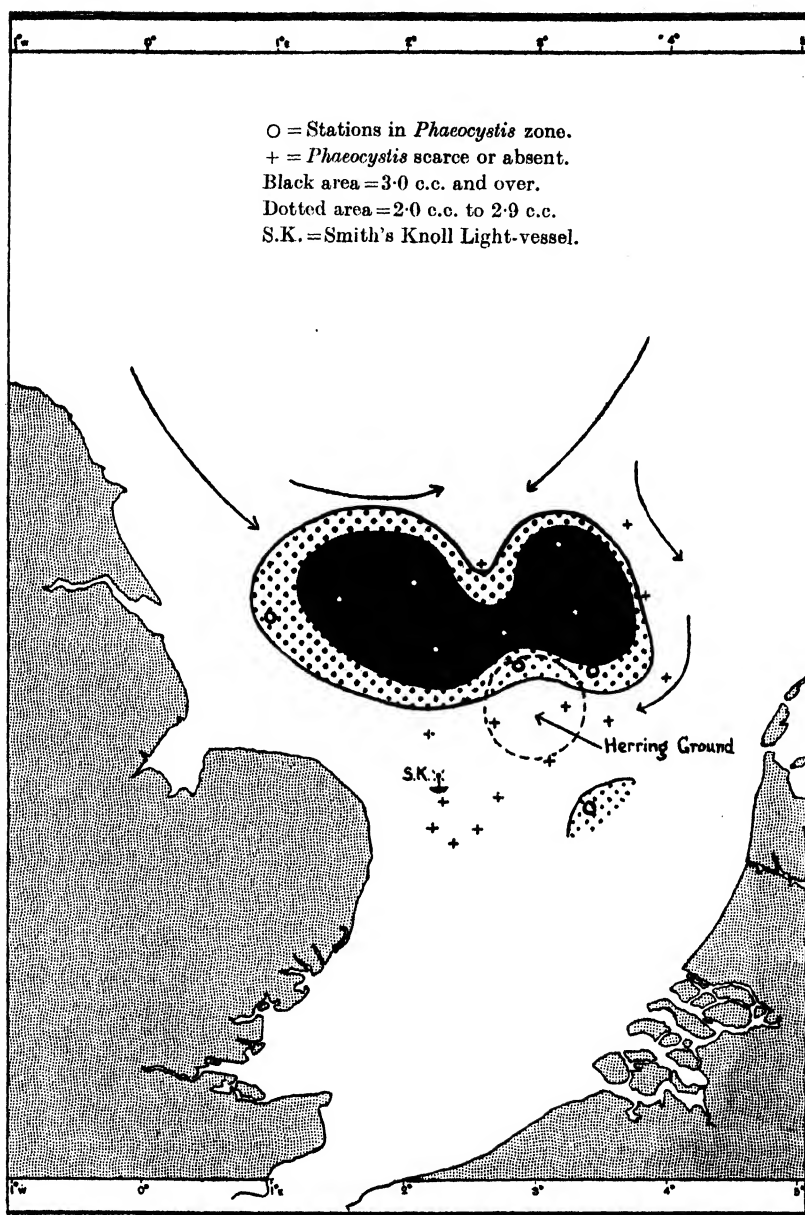
FIG. 7. The distribution of *Phaeocystis* during the period November 6th–9th, 1927. The arrows indicate the assumed migrations of the herring. (Volumes per metre depth—Vertical hauls.)
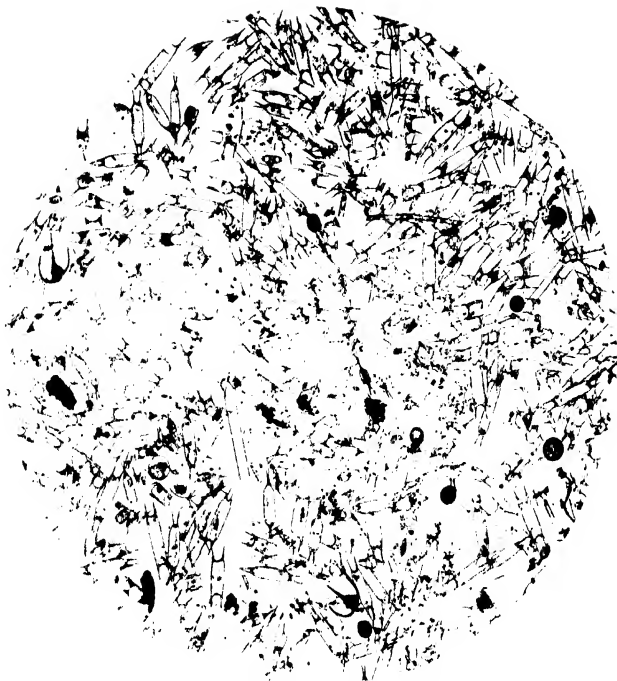
Phot. 1. *Biddulphia sinensis* Grev. (× 28 diam.)

Phot. 2. *Rhizosolenia styliformis* Brightw. (× 28 diam.)

most unusual position (shown in Fig. 7 by a circular area bounded by a broken line).

Dr Hodgson, who has charge of the herring investigations, suggested that we should make a plankton cruise to see if there was any unusual condition of the plankton which might account for it, as we had in previous years found large concentrations of diatoms near that area in November. The research steamer went out and collected plankton samples from this region, and we found a large concentration of *Phaeocystis* extending across the path of incoming shoals for a distance of about 100 miles. It seems very clear that the herring had refused to penetrate this mass of stinking water, and had swum round it as shown by the arrows on the chart, and had thus arrived on the new ground where they were then being caught.

VI. DIATOM CONCENTRATIONS AND HERRING SHOALS.

Diatom concentrations, as previously mentioned, also give rise to a discoloration of the water, and to the so-called "baccy juice." We have as yet found no very clear evidence that they also act as barriers in the same way as *Phaeocystis* does. We have actually found herring feeding extensively on the large diatom *Coscinodiscus concinnus*. Some naturalists have noticed the presence of patches of *Rhizosolenia* on herring grounds, and found that the catches of herring in those areas were poor. Pearcy (7) as long ago as 1885 noticed this off the Shetlands, and recently Hardy (1 and 2), a former colleague of ours, also noticed the same phenomenon.

As most diatoms have their principal flowering period in spring when the herring fishery is small, their effect in any case would not be serious; but there are two North Sea diatoms—*Rhizosolenia styliformis* and *Biddulphia sinensis*—which have their largest maximum towards the end of October or in November.

Biddulphia sinensis Grev. (Pl. XXI, phot. 1) has an interesting history, being a comparatively recent introduction to the North Sea. It is an Indo-Pacific coastal neritic form, which suddenly appeared in the eastern North Sea in 1903. The theory advanced by Ostenfeld (6) is that it was transported there by some ship, either attached to the bottom or in the water of the hold. Since that time it has become firmly established, and is now to be found in large concentrations regularly every autumn. Its centre of abundance is usually in the eastern North Sea near the mouth of the River Elbe and rarely extends sufficiently far westwards for it to have any effect on the herring approaching our coasts. We have carried out plankton surveys for diatom masses during November for a number of years, and the farthest west we have found large concentrations of *B. sinensis* was in 1924 and this happened to be an exceptionally good herring year. We can, I think, rule out this diatom as a menace to the herring.

It is interesting to note the effect on this neritic diatom of the Atlantic

water entering the North Sea through the Straits of Dover. The latter extends north-eastwards as a tongue of higher salinity than the surrounding water and on this occasion practically cut the *Biddulphia* mass into two sections (Fig. 8).
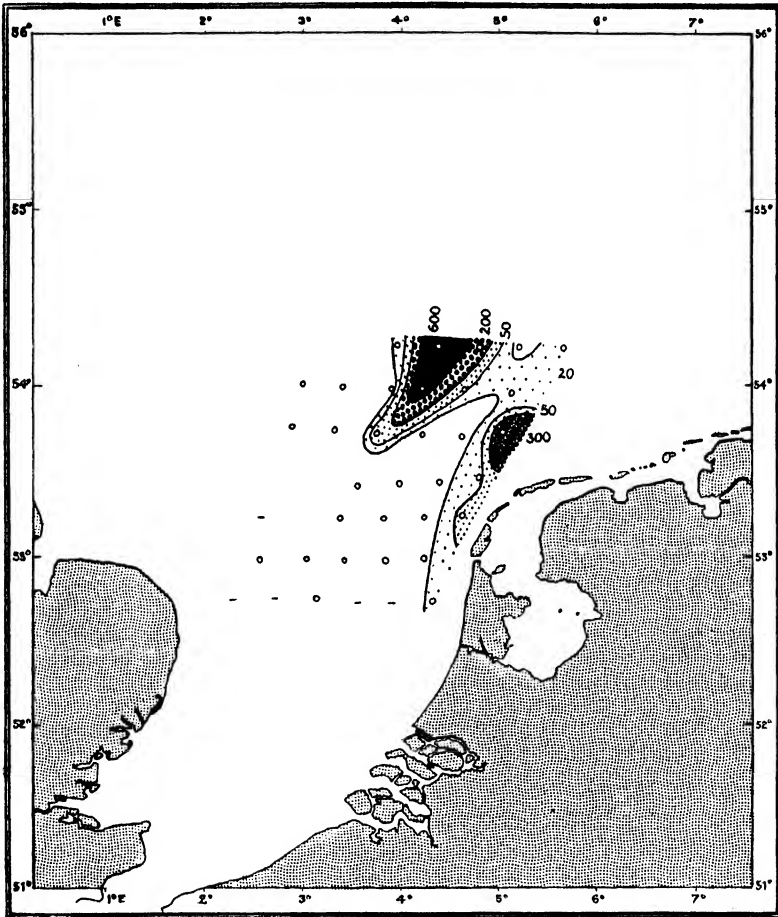
FIG. 8. The distribution of *Biddulphia sinensis* in November, 1924.
Nos. = thousands per cubic metre.

R. styliformis Brightw. (Pl. XXI, phot. 2) is an oceanic diatom which enters the North Sea from the Atlantic from the north in spring, and usually comes to rest near the south-west spit of the Dogger Bank. We have found large concentrations here in November during a number of years. It is also commonly met with on the eastern side of the North Sea. Fig. 9 gives a general idea of the migrations of this diatom. When the main masses enter through the Orkney-Shetland channel we probably get larger concentrations
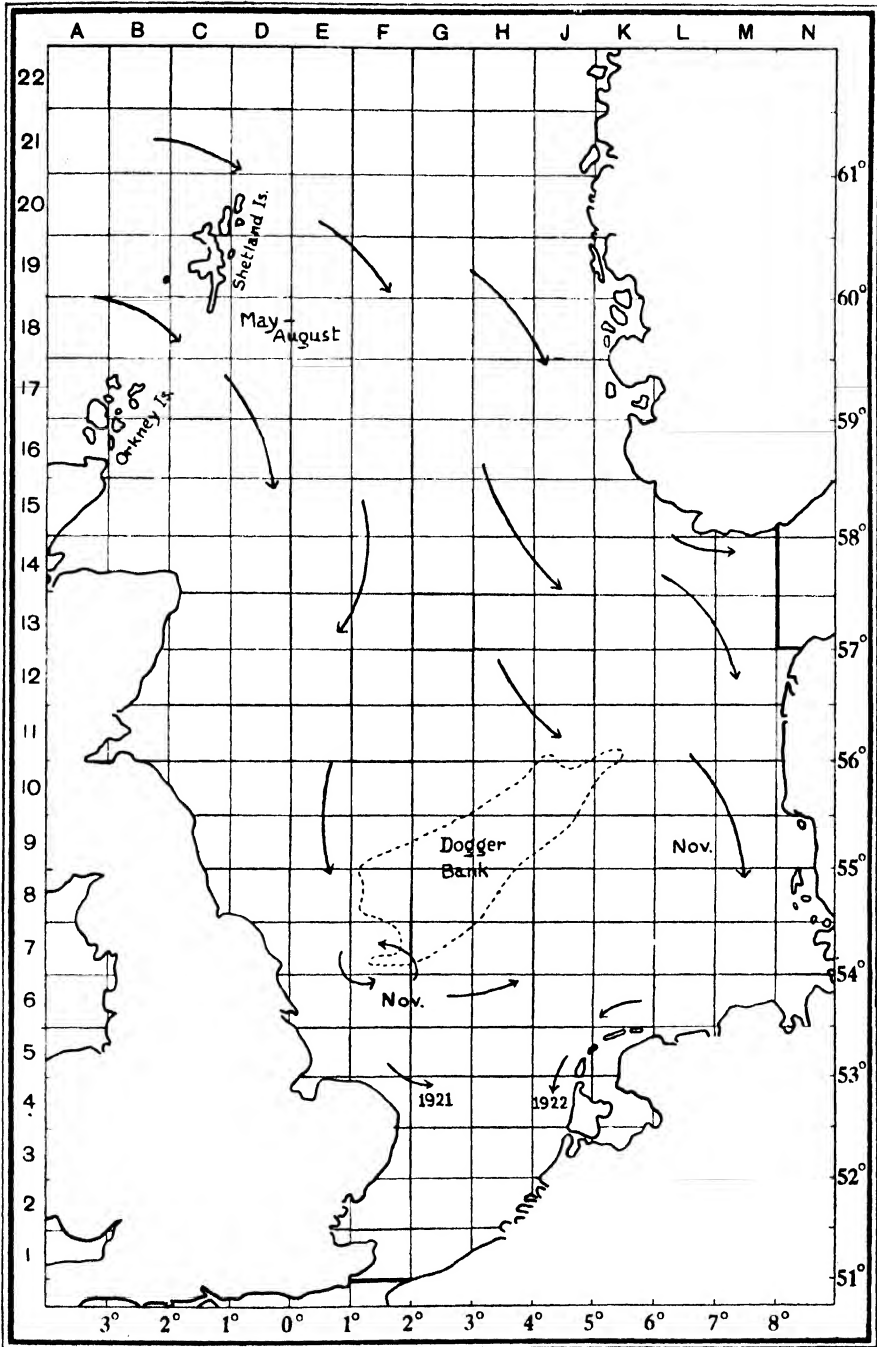
Fig. 9. The migrations of *Rhizosolenia styliformis* in the North Sea.

on our side of the North Sea than when the main influx is north of the Shetlands. In the latter case the masses probably make a wider sweep round and become concentrated in the eastern North Sea off the Jutland coast.

The constant presence of *R. styliformis* near the south-west spit of the Dogger Bank (Fig. 10) in autumn is probably due to a hydrographic swirl
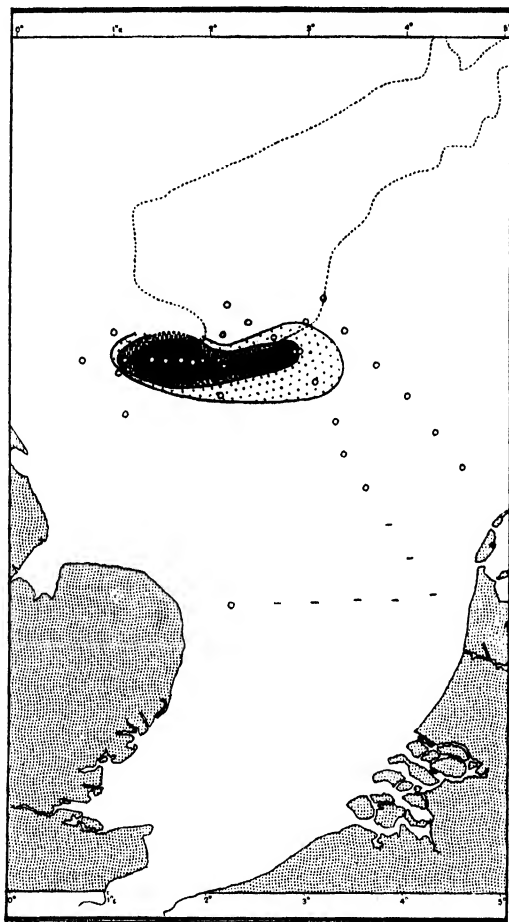
Fig. 10. The distribution of *R. styliformis* during November, 1925.

which is very frequently present there. Other workers have found that oceanic diatoms can flourish on banks such as this one, due to the vertical currents set up along the edge of the bank producing conditions favourable to the growth and multiplication of the diatom. Occasionally—probably in the absence of a swirl—the *Rhizosolenia* concentration passes by the south-west spit and turns eastward just north of the Norfolk coast, in such a position that it might act as a barrier to the herring; we found *Rhizosolenia* in this

area in October, 1926, but there was no noticeable effect on the herring landings. In one exceptional year (1922) *Rhizosolenia* was present towards the eastern side of the Southern Bight in November (Fig. 11), but scarcely in a position to impede the migration of the herring to our coast. Had it drifted there from the west it must have passed across the incoming shoals of herring,
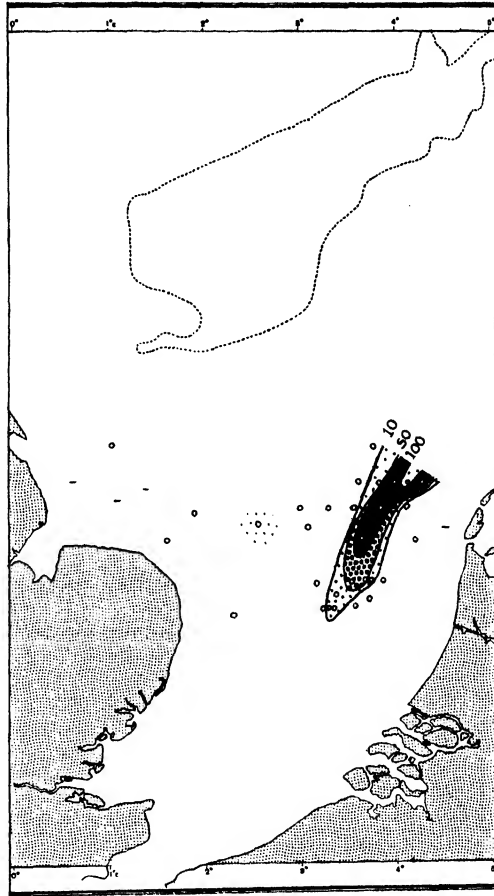
FIG. 11. The distribution of *R. styliformis* during November, 1922.

but it had undoubtedly arrived from the east as there was associated with it quite large numbers of *Biddulphia sinensis* which, as I pointed out earlier, has its centre of abundance round the mouth of the Elbe.

I do not think that *Rhizosolenia* has much influence on the shoaling of herring in English waters. Its normal habitat at the critical period is near the south-west spit of the Dogger Bank, and if it does act as a barrier there to some herring, and cause them to swim round the concentration, it seems

probable that this is a normal occurrence and thus has no appreciable effect on the normal migration. Its absence there *may* have an influence on the landings and it is perhaps significant that in the exceptionally good herring year of 1924 *Rhizosolenia* was almost absent. Against this, however, it should be mentioned that *Rhizosolenia* has always been found low in the water especially during November; the percentage being 4 per cent. at the surface, 28 per cent. in mid-water, and 68 per cent. on the bottom. It would therefore not constitute a fully effective barrier to the progress of the herring, as the latter might swim over the obstruction.

VII. Conclusion.

These observations will give some idea of the factors at work which might influence herring shoaling; the presence or absence of food, the occurrence of a maximum of *Phaeocystis* at the critical period, and an alteration in the direction of the wind. Factors such as these show how difficult the work of forecasting the yield of a herring fishery can be, whether the latter will be a good, bad or a normal one. During the last two years, Dr Hodgson has made forecasts of the probable yield of the East Anglian autumn fishery which proved remarkably accurate (4, 5), but the intervention of *Phaeocystis* in any year might completely upset his calculations.

REFERENCES.

(1) **Hardy, A. C.** "Notes on the Atlantic plankton taken off the east coast of England in 1921 and 1922." *Publications de Circonstance*, No. 78, 1923.

(2) **Hardy, A. C.** "The herring in relation to its animate environment, Part II. Report on trials with the plankton indicator." *Ministry of Agric. and Fisheries, Fish. Invest.* Ser. II, 8, No. 7, 1925.

(3) **Hodgson, W. C.** "Some spawning places of the herring of the southern North Sea." *Journ. du Conseil*, 3, No. 2, 1928.

(4) **Hodgson, W. C.** "Prospects for the East Anglian autumn herring fishery in 1929." *Fishing News*, Sept. 28th, 1929.

(5) **Hodgson, W. C.** "Prospects for East Anglian herring fishery." *Fishing News*, Sept. 20th, 1930.

(6) **Ostenfeld, C. H.** "On the immigration of *Biddulphia sinensis* Grev. and its occurrence in the North Sea during 1903–1907." *Medd. fra Kommissionen for Havundersøgelser*, Ser. Plankton, Bd 1, No. 6, Copenhagen, 1908.

(7) **Pearcy, F. G.** "Investigations on the movements and food of the herring with additions to the marine fauna of the Shetland Isles." *Proc. Royal Physical Society of Edinburgh*, 8, 389, 1885.

(8) **Savage, R. E.** "The macroplankton of the plaice egg cruises, 1920–21." *Min. of Agric. and Fisheries, Fish. Invest.* Ser II, 5, No. 6, 1923.

(9) **Savage, R. E.** "The influence of *Phaeocystis* on the migrations of the herring." *Min. of Agric. and Fisheries, Fish. Invest.* Ser. II, 12, No. 2, 1930.

A COMPARATIVE STUDY OF THE ALGA FLORA OF TWO SALT MARSHES. PART I

By NELLIE CARTER.

(From the Botanical Department, East London College.)

(With two Figures in the Text.)

CONTENTS.

I. INTRODUCTORY.

THIS investigation owes its inspiration to the late Prof. Yapp, since it was started at his suggestion in 1925. It was his wish that a record of the alga flora of the salt marsh at the estuary of the Dovey should be added to the work which he had initiated many years previously in that region (Yapp, 4). Since the writer is stationed at some distance from the Dovey marshes, it seemed advisable to select another salt marsh near at hand in order to obtain a general idea of the algae inhabiting salt marshes. For this reason a small area of salt marsh on Canvey Island in Essex has been kept under observation for about 3 years, visits being made at intervals of approximately 6 weeks. The Dovey salt marsh has been studied during a rather shorter period. From September, 1927 to September, 1928, visits were made at about 6-8 weeks

intervals; before and since these dates, visits were more or less sporadic. By systematic collecting in these two regions, therefore, a general idea of the algae of salt marshes has been obtained, and some interesting comparisons can be made and differences noted. The work was made possible by a grant from the Royal Society, which is here gratefully acknowledged.

II. The topography of the two marshes.

The two marshes differ widely in their geographical position, their geology, and in their phanerogam flora. In the case of the Dovey salt marsh, a very detailed geological and ecological account has been published by Yapp, Jones and Johns (4). The Dovey drains an area of slaty rocks and coarse grits, usually deficient in lime, and the deposits in the estuary are fairly coarse and form a firm substratum on which one can walk with comparative ease when the tide is out. The salt marsh at Canvey is on the north bank of the Thames, and the particular area kept under observation lies on the south side of Benfleet Creek, about 2 miles east of South Benfleet. The area drained by the Thames is very different geologically from that drained by the Dovey, and the deposits in the estuary are very fine and form a sticky tenacious mud. In the Dovey estuary the part of the marsh vegetated by phanerogams slopes gently down to the bare tidal mud except where erosion and undercutting have been going on (see Yapp, 4), and *Glyceria maritima* can easily colonise the silt which stretches out towards the river bed. In the Thames estuary, very different conditions prevail[1]. Here the salt marsh is broken up by deep channels, so that there is often a sheer drop of 15 ft. or more from the level of the phanerogam vegetation to the bare mud in the larger channels, although in the smaller channels the difference in the level is sometimes quite comparable with that on the Dovey marsh. Locally, there may be a more gradual slope down to the bottom of the channel, but even where a sharp difference in level would not prevent one walking out on to the open mud when the tide has receded, its extreme stickiness would render such a venture difficult. The difference in the substratum of the two marshes is therefore very apparent.

## III. The phanerogam vegetation and its zonation.

The zonation of the phanerogams in the Dovey marshes is described by Yapp (4). Starting from the lowest part of the marsh, the zones which can be recognised are the Salicornetum, Glycerietum, Lower Festucetum, Upper Festucetum and Juncetum. There seemed to be some doubt as to whether the Juncetum or the Upper Festucetum is the highest zone. The collections on the Dovey marsh were made at Ynyslas at a point a little west of *A* on

---

[1] I am informed by Mr Smith, of East London College, that this difference is probably due to differences in the scour of the tide, which sweep past, and not up, the narrow estuary of the Dovey, whilst in the Canvey marsh, the scour is stronger, because the tides sweep up the broad estuary of the Thames.
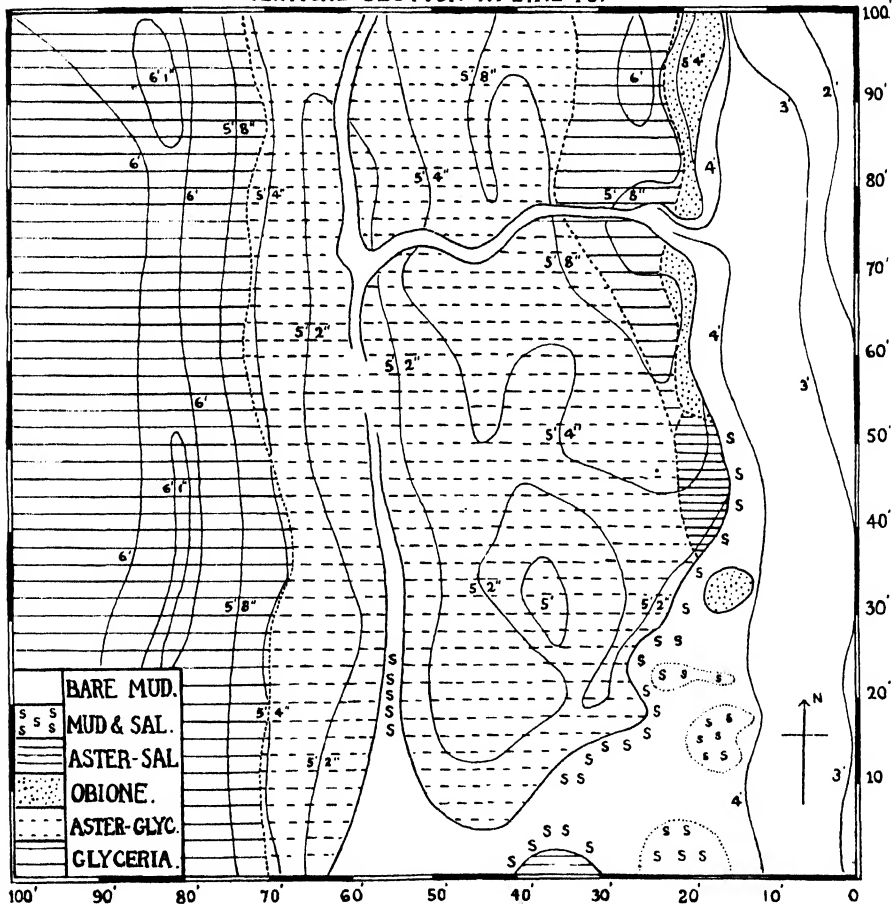
CANVEY AREA No. 1
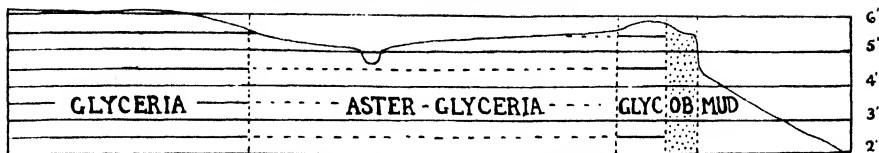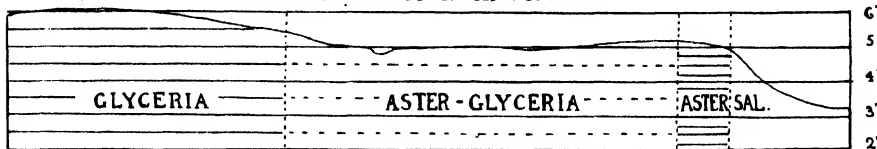
FIG. 1. Map to show the zonation of the phancrogams in a small area of salt marsh near Benfleet‚ at Canvey Island, Essex. Horizontal scale in feet; contour lines in feet and inches measured from an arbitrary zero point in the channel to the right of the map. Zero point of this map not strictly comparable to that of Area No. 2 (Fig. 2). For valuable assistance in the preparation of this map and also that reproduced as Fig. 2, I am very greatly indebted to Dr F. M. Haines.

Fig. 4, p. 35 in Yapp (4), and samples were taken from all the zones recognised by Yapp. The phanerogams here form a compact turf (with the exception of the Juncetum) which is kept short and close by sheep grazing, and in which algae play a very subsidiary part. There is an abundance of algae between the plants, but the phanerogams form the most important part of the vegetation except for a few local patches rarely more than a few inches in diameter, in which algae alone may be in possession.

At Canvey it is difficult to detect zonation in the phanerogam flora at first sight. The whole marsh seems to be covered by a coarse closed community dominated by *Glyceria maritima* Wahlb., with *Triglochin maritimum* Linn. and *Limonium vulgare* Mill. in some abundance, and occasional *Cochlearia anglica* Linn. and *Plantago maritima* Linn. The plants form a rank growth 12–18 in. high which is not grazed and which, like the Dovey salt marsh, is interspersed with pans and channels. The channels are almost invariably fringed with a bushy growth of *Obione portulacoides* Mog. The force of the tidal waters is so strong that for the most part lower and less stable communities are unable to maintain themselves, and the channels are usually cut cleanly and deeply into the compact growth, the fringe of *Obione* being the only other zone recognisable. In occasional spots, an intermediate zone can be distinguished at a slightly lower level between this *Glyceria* zone and the deep channel bottom, taking the form of a shelf with its seaward margin gently rounded or abruptly dropping to the soft mud below. This shelf, which may or may not bear phanerogams, is at certain times of the year covered with algae. In the most favourable spots four or five zones, corresponding to different levels of substratum and bearing different phanerogam vegetation can be distinguished. In one such local area, described as Area No. 2 (Fig. 2), there was an abrupt drop of about 8–12 in. from the *Glyceria* zone down to a shelf, fringed at the landward margin by *Obione*, and gently sloping to the seaward for about 6 ft. This shelf is colonised by *Aster Tripolium* Linn. and *Salicornia* sp. which form an open community, the soil between the plants being covered with algae. There is a shallow step of about 6–8 in. from the *Aster* shelf to the general bottom of the channel in this particular spot, and part of the slightly higher mud in the channel is colonised by a pure growth of *Salicornia herbacea* Linn. As regards phanerogams the zonation of the Canvey marsh is therefore *Salicornia*, *Aster*, *Obione* and finally *Glyceria*. No analyses of the turf in the upper zone referred to as the *Glyceria* zone have been made, but it is apparent from a superficial examination at the time of flowering that *Glyceria* is the dominating grass and that other plants are quite subsidiary. The striking difference in the phanerogam vegetation at Canvey and the Dovey estuary lies in the fact that whilst in the latter locality the *Glyceria* zone immediately succeeds *Salicornia* in the lower levels, at Canvey these zones are separated by two intermediate phanerogam zones, dominated by *Aster* and *Obione* respectively. It is probable that this difference in position

of *Glyceria* on the two marshes does not really represent a difference in level with reference to the tides (see p. 368). On the other hand, it is almost certain that the vertical position of *Glyceria* is quite comparable in the two localities, and that zones equivalent to the Armerietum, Festucetum and Juncetum are
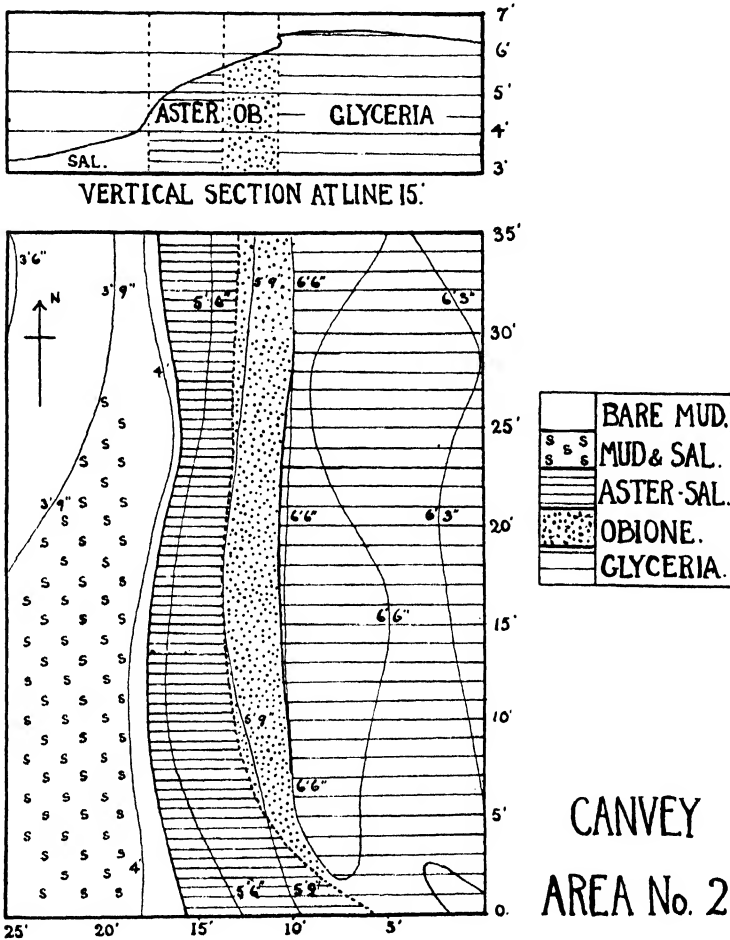

FIG. 2. Map to show the zonation of the phanerogams on a small piece of salt marsh near Benfleet, at Canvey Island, Essex. Horizontal scale in feet; contour lines in feet and inches measured from an arbitrary point in the channel to the left of the map. Zero point probably about 4 in. higher than in Area No. 1 (Fig. 1).

wanting at Canvey, since the sea wall is maintained at the edge of the *Glyceria* zone[1]. The *Aster* and *Obione* zones at Canvey are then interpreted as zones

[1] It has been pointed out subsequently to the writer that on other parts of the Canvey marsh local areas occur, colonised by *Armeria maritima* and *Festuca rubra* respectively, which represent zones higher than the general *Glyceria* community. These areas were afterwards examined, but the turf was so compact that few algae were obtained from it (see also footnote, p. 359).

intermediate between the *Salicornia* and *Glyceria* zones, which are not represented at Ynyslas.

At Canvey, *Glyceria* was only observed in one spot to approach the open mud, so that the *Aster* and *Obione* zones were wanting. Here silting up was evidently going on at the head of a channel. There was no deep cutting into the turf by the channel, the vegetated area sloping quite gently down to the open mud (Fig. 1, bottom). An extensive stretch lower in level than the ordinary *Glyceria* zone was apparent, being in part even lower than the *Aster* zone. This area was covered with *Glyceria*, but was abundantly interspersed with *Aster* (*Aster-Glyceria* in Fig. 1). The *Glyceria* in this region tended to approach the open mud. In the opinion of the writer this area has probably quite recently subsided, and may be still gradually sinking in level.

This short account of the phanerogam vegetation at Canvey is not intended to be comprehensive, and is only given to show that there are, even in the higher plants, marked differences as compared with the Dovey estuary. Floristically, the Canvey marsh resembles the marshes of the Norfolk coast (Marsh, 3), rather than the Dovey marsh, but the zonation in the particular locality studied is not exactly the same. Correlated with the difference in the phanerogam flora at Canvey and at Ynyslas is a striking difference in the alga flora, but it is quite probable that light and space relations are also very important in determining these differences.

In the Dovey estuary, all the zones are essentially closed communities as regards phanerogams, except for the Salicornetum; in the Glycerietum also there is at times considerable bare soil between the plants. The higher zones, dominated by *Armeria* and *Festuca*, consist of a grassy sward in which the plants are very close together, but as they are cropped short by sheep the tiny spaces between them receive considerable illumination and conditions for algal growth are favourable. Consequently algae are abundant, but since they are tightly wedged in between the phanerogams they are not conspicuous at first sight. In the Juncetum, because the plants have slender cylindrical leaves rather than leaf rosettes, considerable light can reach the ground, and there is, in addition, much bare ground between the plants available for colonisation by algae. Thus the conditions are very favourable here to the growth of algae, and the area of soil covered by algae is relatively much greater than in the turf zones.

At Canvey, the *Salicornia* and *Aster* zones are both open communities and there is much bare soil receiving illumination, so that in the appropriate season algae can develop abundantly. Here algae form a much greater proportion of the obvious vegetation than on the Dovey marsh. The soil of the *Obione* zone receives less illumination because of the shrubby nature of the *Obione* plants, and the algal vegetation is often less abundant. The *Glyceria* zone, however, is very different because of its tall close growth of grasses which, on dying down, cover the ground with their prostrate haulms. This is further

aided by the periodic flooding of the area by the tide. Very little of the actual soil between the plants can therefore receive any illumination, and algal growth is scanty, such algae as do occur in this zone living mostly as epiphytes on the prostrate and dead remains of phanerogams, rather than on the soil itself. The higher plants of the various zones, by controlling light and space relations, may therefore have a great influence on the algal vegetation.

IV. THE ZONES AND THEIR ALGAL INHABITANTS[1].

Ynyslas.

A. *Salicornietum, and associated mud flats free from phanerogams.*

As a rule there is little algal vegetation visible in this zone with the exception of strands of *Enteromorpha prolifera* which seem to be present as unattached tangles; that is, the plants have no special basal holdfast, but are merely hanging on the *Salicornia* plants or loosely lying anchored in the mud. The mud itself occasionally shows a brownish film in which diatoms may be suspected; or, especially in late summer, a blue-green film may occur locally, in which *Microcoleus chthonoplastes, Oscillatoria sancta* and *O. corallinae* are the most important forms. Often, when there are no visible algae on the surface, isolated filaments of the above-mentioned Cyanophyceae may make their appearance if a sample of the mud is exposed to the light for some time. *Microcoleus acutirostris*, the diatom *Scoliopleura tumida* and sometimes *Euglena limosa* may also be present in the mud.

At certain times (March and August, 1928) the mud in some sheltered inlets was permeated by a species of *Vaucheria*, which, when it fruited, was identified as *V. sphaerospora* Nordst. This is not a general constituent of the zone, however, and only occurred locally. A slender form of *Rhizoclonium* accompanied it.

Drift material lying on the bare mud often included fragments of Rhodophyceae and Phaeophyceae entangled with fragmentary *Sertularia* and other animal remains. Such drift algae were ignored, since they had obviously only been deposited on the shore by the receding tide, and if not already dead, or in bad condition, could certainly not live long. It is quite otherwise, however, with *Enteromorpha*, which seems to be present at most times of the year[2]. This alga, although not attached to the substratum, is quite healthy; it remains fresh for several days and continues to evolve oxygen for some time after collecting. It seems probable that it should be considered as a normal inhabitant of the marsh, and in quite a different category from the occasional drift forms which are washed up. The growth of *Enteromorpha* is

---

[1] A list of all the algae found will be published as Part II, and an ecological treatment of the algal communities as Part III.

[2] At Ynyslas, in July, 1927, 1929 and 1930, the marginal mud flats were free from *Enteromorpha*, and there was no drift algal material of any kind to be seen.

very different on the Canvey marsh as compared with Ynyslas. In the first locality it forms a blanket, growing on the surface of all the available mud at a suitable level. At Ynyslas it is in the form of long strings, the algal filaments tangled into more or less rope-like masses, which become loosely anchored.

Whilst *Enteromorpha prolifera* is the usual form of unattached alga found lying on the bare mud, under certain conditions *Rhizoclonium* is present. In August, 1928, large masses of this alga, 3 or 4 ft. in diameter, lay in the tiny inlets of the shore. The alga was healthy and almost pure, except for a filament or so of *Microcoleus chthonoplastes* or a little *Enteromorpha percursa*. It is a peculiar fact that although further out on the mud many tangles of *Enteromorpha* were anchored, these *Rhizoclonium* masses lying near the shore included no *Enteromorpha prolifera*. The two forms were living quite independently of each other.

The origin of this drift alga, whether *Enteromorpha* or *Rhizoclonium*, is problematical, and could only be decided by more frequent observation than the present writer could make. It might possibly have its origin in the higher zones of the marsh such as the Glycerietum or Armerietum, and be deposited on the lower mud flats after having been washed down by high spring tides. Even if this is so, however, one must conclude that after being deposited on the mud, the alga continues to live and increase considerably in bulk in its new habitat, for the actual mass of alga found there is much greater than could be explained by the mere washing down from higher levels. As regards *Enteromorpha*, this alga is common on the mud flats nearly all the year round, whilst in the Glycerietum and Armerietum it is very rare, especially in the winter months, when it is practically absent. It appears, therefore, that *Enteromorpha* lives its life on the mud flats independently of any other zone. *Rhizoclonium*, on the other hand, is a frequent constituent of the adjoining zones at most times of the year, yet it only occurred very rarely on the mud flats. Although it is a form of the same species, *R. hieroglyphicum* subsp. *typicum*, the mud flats form is very much stouter than that usually found amongst the grasses of the higher zones of the marsh, reaching a diameter of $38\,\mu$. In the adjoining Glycerietum it is rarely more than $24\,\mu$ in breadth. These facts would therefore seem to suggest that mechanical washing away of algae by the tides from higher levels does not materially add to the bulk of alga on the mud flats, and that the algae found there are to be considered as real inhabitants of that zone. Their more detailed biology must be left for future workers.

B. *Glycerietum.*

This is usually a fringing zone at the margin of the marsh, and, as stated by Yapp (4, p. 68) it is a pioneer association and is open at first. There seems to be, however, to the landward side of the marsh, a second strip of what is

apparently Glycerietum. It lies between the Juncetum zone and a deep channel, and its chief constituent is obviously *Glyceria maritima*. I have not been able to find any mention of this zone in Prof. Yapp's paper, and believe it quite possible that there has been a recent sinking in level at this point, which has enabled *Glyceria* to become the dominant plant. The area in question is wetter than the surrounding Armerietum and Festucetum, and its algal flora is different from that of the marginal Glycerietum, probably because of the less disturbed conditions prevailing there. For this reason it seemed advisable to consider the two regions separately.

(a) *Marginal zone.* The general impression of this region is conspicuous bareness. The frequent stretches of soil between the *Glyceria* plants often show no evidence of the presence of algae. Microscopical examination of a sample, especially after standing for some time, may reveal the presence of *Navicula cincta* var. *heufleri*, *N. (Schizonema) Grevillii*, or *Nitzschia rigida*, *Oscillatoria corallinae*, *Microcoleus acutirostris* or *M. chthonoplastes*, but these are never present in great quantity.

In the winter months, November–January, *Vaucheria* is locally present, penetrating the mud between the *Glyceria* plants, but *Rhizoclonium* is a more constant constituent, sometimes forming pure mats, an inch or so in diameter, between the phanerogams. In September, 1927, *Enteromorpha percursa* was dominating in local spots, although, on the whole, *Rhizoclonium* was the more abundant form. Definite algal mats covering the soil between the higher plants are not especially frequent in this zone, the algae for the most part being rolled by the tide into tangled strings or ropes which hang on the *Glyceria* plants, or are caught in the mud. These tangles usually include a mixture of *Rhizoclonium* and *Enteromorpha prolifera*. The *Rhizoclonium* is similar to that in the turf. The fact that in this zone the algal ropes include a mixture of species, whilst on the mud flats the species usually occur pure, seems to support further the contention that there is little replenishing of the mud flat inhabitants by washing down from higher levels. In the early spring, *Pylaiella litoralis* is frequently anchored in the mud between the plants.

(b) *Nearer Juncetum.* *Vaucheria* is the most conspicuous alga here at most times of the year except in summer, when *Microcoleus chthonoplastes* and *Lyngbya aestuarii* become much more important, and dominate extensive stretches between the grasses. *Rhizoclonium* and *Enteromorpha percursa* may occasionally be important locally, but they play in general only a very subsidiary part.

C. *Armerietum.*

Three algae seem to compete for space between the phanerogams in this region, namely, *Vaucheria*, *Rhizoclonium* and *Enteromorpha percursa*. *Rhizoclonium* was often dominating completely November–July, but the other two forms were nearly always present and sometimes locally dominant. *Vaucheria*

and Cyanophyceae were very important in July and August, 1928, when, after a period of drought the marsh was exceedingly dry. The dark blue colour of the algal tufts contrasted very prettily at that time with the rich red hue of the *Armeria* plants between which they were growing, and it was obvious to the naked eye that such algae as *Rhizoclonium* and *Enteromorpha percursa*, which are much paler in colour, were absent. It is indicated that drought and lack of soil moisture have much to do with the exclusion of these forms, for, in the moister turf near the edges of the marsh, which is more frequently submerged by the tides, both algae were present in some quantity. It is well known that Cyanophyceae have great capacity for resisting drought, and *Vaucheria* probably tolerates dry conditions better than the other Chlorophyceae because its filaments penetrate the soil to a greater depth, for *Rhizoclonium* and *Enteromorpha* are usually quite superficial, or penetrate the soil only very slightly. Locally, and especially in summer, slender filaments of *Enteromorpha prolifera* may form a carpet on the bare soil between the higher plants. Cyanophyceae, of which *Microcoleus chthonoplastes* and *Lyngbya aestuarii* are the most important, but amongst which *Gloeothece palea*, *Lyngbya lutea* and *Oscillatoria corallinae* also occur, may dominate locally at any time of the year, but they become especially prominent in late summer. In the early spring months *Pylaiella litoralis* or *Ulothrix* spp. may be present near the river margin, especially if the escarpment cuts into this zone. Ropes of drift are sometimes present and usually consist mainly of *Enteromorpha prolifera*, amongst which are a few strands of *E. percursa* and *Rhizoclonium*.

D. *Lower Festucetum.*

Vaucheria and *Rhizoclonium* struggle for dominance in this zone, and, as far as observations go, *Vaucheria* seems to be more successful in September–March and *Rhizoclonium* in May–July. In the wetter winter months such Cyanophyceae as *Oscillatoria corallinae*, *O. sancta* and *Microcoleus chthonoplastes*, and the diatom *Nitzschia bilobata*, *Navicula peregrina* and *N. formosa* may occur with the larger algae, the blue-greens very commonly associated with *Vaucheria*. At this time of the year also, *Enteromorpha percursa* was sometimes locally dominant, whilst it was not observed in the summer months. The green algae in late summer frequently overlie a tough stratum composed largely of Cyanophyceae in which *Lyngbya aestuarii*, *Hydrocoleum lyngbyaceum*, *Gloeothece palea*, *Nodularia Harveyana*, *Microcoleus chthonoplastes* and *Phaeococcus adnatus* occur, and in dry conditions this community of blue-greens may become more prominent and tend to oust the Chlorophyceae.

E. *Upper Festucetum.*

This zone is possibly the highest, and its algal flora probably approaches more nearly that of ordinary non-saline soils. It was not given so much attention, therefore, as the other zones, and most of the data relate to the

summer months. At this time of the year (May–August), Cyanophyceae predominate amongst the algae. *Rivularia* and *Nostoc* are very important forms, but the latter is most abundant in the wettest months of the year. In March it was present as very large gelatinous masses, the colonies an inch or more across, and microscopic examination of the turf revealed the presence of numerous smaller individuals as well. In dry weather, as in the summer months, June–August, the large colonies of *Nostoc* which had been so conspicuous earlier, became very withered, black and brittle. *Rivularia* is very frequent at all times of the year, but, since its colonies are smaller, it is never as conspicuous as *Nostoc*. Even in summer microscopic colonies of *Nostoc* seem to be important.

The turf formed by the grasses is very close. Mosses[1], of which there are at least two species, are present in some quantity and form a considerable proportion of the turf. As a general rule there is a thin gelatinous stratum of Cyanophyceae overlying the lower parts of the mosses or phanerogams; the *Rivularia* colonies are scattered over such bare patches as occur on the soil between the higher plants, over which large *Nostoc* colonies are strewn. In the thin gelatinous stratum of Cyanophyceae one of the most important forms is *Hydrocoleum lyngbyaceum*, which can be found at most times of the year, whilst *Anabaena*, *Lyngbya lutea*, *Phormidium* spp. and *Gloeothece* become more abundant in late summer. *Phaeococcus adnatus* may usually be found at all times of the year. Chlorophyceae do not seem to play a very important rôle in this zone, probably owing to the dryness which results from the very rare submergence by tides. In the winter months *Vaucheria* and *Rhizoclonium* may dominate in local spots, but in summer only fragments of these algae were found.

F. *Juncetum.*

This zone seems to exhibit more stability in its algal flora than any other. Because of the stiff spiny nature of the *Juncus* plants there is not the same disturbance from sheep grazing as in the other zones. The habit of the *Juncus* plants is such that there is considerable soil between them on which algae can develop; the cylindrical nature of the *Juncus* leaves (as opposed to the tufted habit of the grasses and the rosettes of *Armeria* and *Plantago* of other zones) allows good aeration and access of light. The tall rushes also serve as a protection from excessive transpiration, so that the algae on the surface of the Juncetum are bathed in a moist atmosphere when those of lower zones are suffering from drought and exposure because the turf in which they are living is cropped short by the sheep. Since the conditions are therefore more uniform, there is little seasonal variation, and the algal flora is fairly constant in its composition. *Vaucheria* and *Rhizoclonium* are present in considerable

---

[1] I am deeply indebted to Dr W. Watson for the names of these two mosses. They are *Pottia heimii* (Hedw.) Fuernr. and *Amblystegium serpens* (L.) Br. Sch. var. *salinum* Carr.

quantity at all times, usually growing in separate areas, *Vaucheria* forming dark velvety stretches, and *Rhizoclonium* close mats, paler in colour. Locally *Sphacelaria* may form a light brown velvety growth, but these small patches are usually quite subsidiary to the larger areas occupied by the other two species. A considerable proportion of the surface of the soil is obviously occupied by Cyanophyceae, amongst which *Lyngbya aestuarii*, other *Lyngbya* spp. and *Microcoleus chthonoplastes* are the most important.

This zone was also unique in its possession of three larger algae, two members of the Rhodophyceae and one of Phaeophyceae. *Catenella Opuntia* and *Bostrychia scorpioides* occurred locally in the Juncetum, and often grew intermingled, forming tangled growths adhering closely as a collar around the base of the *Juncus* plants. A marsh form of *Pelvetia canaliculata* was also frequent at this spot, although it is really quite local. This forms pure stands, except that a ground flora of *Rhizoclonium* or *Vaucheria* is usually present. There was no definite relation to the *Juncus* plants as in the case of *Catenella* and *Bostrychia*, and unlike these two algae also, *Pelvetia* often spreads from the bare soil of the Juncetum for a short distance into the adjoining turf of grasses. These three larger algae were very local in their occurrence. They seem to prefer a stretch of bare mud between the *Juncus* plants for their development. Further towards the mouth of the Dovey, there is a considerable amount of tall grass flourishing between the rushes and here a search failed to reveal any one of them. It may be that when grasses flourish the soil is unsuited to the algae, or it may be that space relations are in question. The obvious fact is that these three algae seem to enjoy the moist soil of the sheltered Juncetum, where there is little competition with higher plants.

Canvey.

Two localities have been kept under observation at Canvey, and, as they seem to provide rather different ecological habitats, they will sometimes be referred to separately.

(1) *Area No.* 1 (Fig. 1). The regions recognised in this locality are as follows (starting from the mud of the channel and going towards the stable ground):

I. Bare mud. The substratum is very unstable, obvious differences in the level of the surface of the mud, its angle of slope, and also in the contour of the margin of the vegetated part of the marsh being very marked during the three years of investigation. *Salicornia*, when present, forms a fringe just outside the limits of the next zone, II. Locally hummocks or islands of a higher level occur, some bearing phanerogams, *Salicornia* appearing first and then *Aster*.

II. A narrow and very local shelf bearing *Salicornia* and *Aster*. This shelf has persisted during three years, and it is probably rising in level since it

bears much more *Aster* now than at the beginning of the investigation. At the present time, however, it is of considerably less area than formerly.

III. A much more extensive area bearing *Glyceria maritima* as the dominant plant, but with a large proportion of *Aster*. In 1928 *Suaeda maritima* was also present in great quantity, but it has subsequently become less common. This region is somewhat lower in level than V and is consequently much wetter. It was only distinguished from V some time after the investigation was started, and it is quite possible that there has been a general sinking in level of this area so that zone III developed secondarily during the period of the investigation.

IV. A zone of *Obione* can also be distinguished but it was not investigated in this area.

V. The general *Glyceria* zone.

(2) *Area No. 2* (Fig. 2). The channel to the left of this area is a "cul de sac," since beyond the top of the map it ends abruptly at the sea wall. Consequently the tidal waters do not run in and out with the same force as in Area No. 1, and, on the whole, the unvegetated part of the substratum is softer because the tidal water tends to stagnate. It shows the following zonation:

I. Bare mud. This is exceedingly soft and almost liquid. Locally there are slightly higher stretches bearing *Salicornia*, and also further out in the channel, islands higher still, on which *Aster* as well as *Salicornia* flourishes. The *Salicornia* zone is much better developed here than in Area No. 1.

II. Next is a zone bearing *Salicornia* and *Aster*. It has become rather smaller by erosion, especially at the north end, in the three years during which it has been kept under observation, and more recently other changes also have been taking place. In 1927 the phanerogams present here included only the two plants mentioned above. At the time of writing *Glyceria maritima* from adjoining land has invaded the entire area and, becoming dominant, has completely altered the character of the zone. The present account refers to the time when it was a pure *Aster-Salicornia* zone.

III. The shelf bearing *Aster* and *Salicornia* slopes very gently inland towards the general *Glyceria* community, from which it is separated by a sharp vertical escarpment about 9 in. high. There is a fringe of *Obione* at the base of this escarpment. The soil is very firm, and the escarpment is also firm. Although the *Obione* plants must serve to protect this escarpment at all times of the year, it is undercut by erosion to a considerable depth (cf. vertical section, Fig. 2).

IV. The general *Glyceria* zone.

The alga flora of these different habitats will be dealt with in the following order:

A. *Bare mud* and *Salicornia*. It is not desirable to separate this into areas with and without *Salicornia*, since the same algae extend through both.

B. *Aster-Salicornia* zone.

    C. *Obione* zone (only investigated in Area No. 2).

    D. *Aster-Glyceria* zone (only represented in Area No. 1).

    E. Upper *Glyceria* zone.

A. *Bare mud and Salicornia.*

The richness of the algal flora of this region, as contrasted with the corresponding zone of Ynyslas is most striking. Numerous diatoms and Cyanophyceae occur here and can usually be distinguished as rich brown, dark blue-green or olive films covering the mud, provided that the tide has receded sufficiently long to allow the films to develop. Exposure to light is important in causing the organisms to rise to the surface of the mud and produce these smooth films. Diatom films of a rich brown colour are very conspicuous, especially in November–January, when all channels show uninterrupted stretches of colour owing to their presence. Such films are present also in summer, but since other algae are then more abundant, they are relatively less striking at this season. These diatom films afford a wealth of species, some of which are present all the year round, but the dominating ones vary according to season. In the winter months (November–March), *Pleurosigma angulatum* and *Surirella gemma* occur to the exclusion of almost everything else, and form pure films of great extent. In the softer mud of Area No. 2, *Gyrosigma diaphanum* may be more conspicuous than either of these two. In the summer months *Scoliopleura tumida* and *Amphora lineolata* become the most conspicuous forms. For further details see Part III.

A bright green film, usually in local spots rarely more than an inch or so in diameter, indicates the presence of *Euglena limosa*. This organism does not seem to be as abundant here as on the banks of the Avon (cf. Bracher, 1).

The Cyanophyceae occur as a rule in local patches and not in such extensive areas as the diatoms. Even when no Cyanophyceae are evident in the field, if some of the mud is collected and exposed to light for some time, isolated blue-green streaks, about the thickness of a hair and 4 or 5 mm. long make their appearance on the surface and can be seen with a hand lens. These prove to be filaments of *Microcoleus chthonoplastes* or even more frequently, *M. acutirostris*, which are evidently sparsely distributed in the mud and rise to the top under the stimulus of light. Sometimes, when the mud is rather moist, a species of *Pseudanabaena* may be more abundant than *Microcoleus* spp. in the marginal mud. This alga may be present in the field as a slaty blue film, or it rises to the surface on standing as a dull smudge. Species of *Merismopedia* are also frequent, though not sufficiently abundant to affect the coloration of the soil.

The more obvious Cyanophyceae ordinarily seen in the field as definite olive films of considerable extent prove, as a rule, to be *Oscillatoria corallinae* or *O. sancta*. Narrow species of *Phormidium* may also be present with the *Oscillatoria* spp. There is some indication that this community of Cyanophyceae

prefers rather firmer mud, since it is developed best on the firmer substratum of Area No. 1. Here, also, the hummocks which are rising in level and will soon bear phanerogams are covered with a tough film of these blue-greens. In the softer mud of Area No. 2, however, the blue-green community is scarcely represented. Some Cyanophyceae are present in zone A, where conditions are suitable, at all times of the year, but they are much more conspicuous in late summer. There are also other Cyanophyceae, however, which are more definitely seasonal. *Anabaena* in August is likely to appear with *Nodularia* sp. or *Phormidium* spp. as rounded colonies of a moist dark blue appearance on the surface of the soil. This also does not occur on the softer mud of Area No. 2.

All the above marginal forms probably require a certain amount of moisture in order to flourish, and are dependent to a large extent on the tides or on drainage water or possibly rain for their supplies. Thus, when weather and tide conditions are such that the surface mud of the channels is thoroughly moist, the diatoms and Cyanophyceae will usually be very abundant. Ordinary neap tides will submerge some of the bare mud, though not nearly as far up as the phanerogams; but sometimes drought and unusually low tides occurring together will result in the surface mud of the channels becoming very dry, even to the extent of cracking. In such conditions, living diatoms and Cyanophyceae are very rare, and the films usually produced by them are absent.

Vaucheria is a conspicuous form inhabiting the bare mud, but it is distinctly local. A firm substratum seems essential to *Vaucheria*; consequently it is entirely wanting in the softer mud of Area No. 2. In Area No. 1 there were often ridges somewhat higher than the surrounding mud. These, being dryer, were always well covered with a dark, almost black growth of *Vaucheria*. Some of the hummocks already referred to are also vegetated with *Vaucheria*, which makes its appearance just before the hummocks are high enough to develop phanerogam vegetation (see pp. 352, 353). The *Vaucheria* siphons often penetrate the mud to a considerable depth, but there is sometimes a quantity of other, more superficial Chlorophyceae, lying on the surface of the mud, such as *Enteromorpha prolifera* or *Ulothrix* spp. In Area No. 1, where the slope was usually very steep, these filamentous green algae are confined to the upper region, on the firmer escarpment leading to zone B, where they form a narrow fringe rarely more than 1 ft. in diameter. In Area No. 2 these superficial algae often lie amongst the *Salicornia* colonising the soft mud, and also on the open mud of the channel for considerable distances all round. Since the flow of tidal water is not so strong here, there is less disturbance, and for this reason the algae can extend further into the channel than in Area No. 1. In both localities this superficial flora of Chlorophyceae is absent in the late autumn and winter months, October–January. Except for an isolated thread or so of *Enteromorpha* or *Rhizoclonium* and for the epiphytes which cover the dead *Salicornia* plants (e.g. *Enteromorpha minima* and *Rhizoclonium*), Chloro-

phyceae are very poorly represented at this time of the year. A striking change comes over the marsh in January or February, when there is a spontaneous development all over the marsh of *Ulothrix flacca*. In Area No. 1 the margin of the escarpment then becomes covered with a silky growth which, when moist, is of a rich blue-green colour. In Area No. 2 this alga festoons all the old *Salicornia* plants and covers the intervening and surrounding mud with a bright carpet. Other more slender species of *Ulothrix* may occur as isolated strands, and *Enteromorpha minima* is very common at this time of the year, but the bulk of the extensive growth is *Ulothrix flacca*. Along the firmer upper slopes towards the *Aster-Salicornia* zone, there may be tufts of a brown alga among the *Ulothrix*; this is probably *Pylaiella litoralis* which hangs in festoons from the escarpment. This striking phase, in which *Ulothrix flacca* plays such a great part, seems to be short lived, and in March the alga becomes considerably less in quantity, whilst at the same time *Enteromorpha prolifera* becomes more prominent. In both Areas, Nos. 1 and 2, the escarpment leading to the *Aster-Salicornia* zone is then clothed with a green carpet of *Enteromorpha*, which persists in general from March to September. At this time a few threads of *Rhizoclonium* may occur amongst the *Enteromorpha*, but there is rarely any bulk of this alga present. A spell of drought accompanied by neap tides may influence the appearance of the *Enteromorpha* carpets as in May, 1927, when the muddy channel became so dry and firm that one could walk on it with ease; on this visit it was observed that *Enteromorpha* was wanting, even at the margins of the escarpment.

The open mud of Area No. 1, apart from the escarpment, was usually free from the larger filamentous Chlorophyceae, with the exception of local *Vaucheria*. On the softer mud of Area No. 2, however, especially in the summer months, *Enteromorpha* seemed to flourish. The form of this alga lying out on the mud was different from that clothing the escarpments. In the latter habitat, the filaments were long and very slender, rarely exceeding 1 mm. or so in diameter. In July and August, however, very stout *Enteromorpha* fronds, tubular, 1 or 2 cm. in diameter, and several inches long, with abundant branches, were to be seen lying in quantity on the soft mud, or more rarely amongst the *Salicornia* plants themselves. This was observed several summers in succession. It is probable that the coarse form of *Enteromorpha* is not different specifically from the more slender marginal form, but, as is well known, the estuarine forms of this genus are almost indeterminate (cf. Part II).

Sometimes the channels cut deeply into the Upper Glyceria zone without the intervention of the *Aster-Salicornia* zone. Then vertical faces of bare mud are produced where erosion has been taking place. Locally erosion or undercutting may cease, and if they are undisturbed for a sufficiently long period of time, such vertical faces may sometimes bear *Vaucheria* or *Enteromorpha*. Even more frequently, however, the diatom *Navicula Grevillii* makes its

appearance, its filaments ramifying amongst the particles of soil and producing a tough surface indistinguishable to the naked eye from bare eroding soil.

B. *Aster-Salicornia zone.*

Diatoms are still very numerous, but, owing to the prominence of larger algae they do not play such a conspicuous part in the alga flora. Cyanophyceae become very striking in late summer. The diatoms most commonly occurring are *Navicula formosa, Scoliopleura tumida, Navicula vacillans, N. cincta* var. *heufleri, Gyrosigma Spenceri* and *G. attenuatum* var. *scalprum.* In July, *Amphora lineolata* often becomes the most abundant diatom and in July, 1928, it produced a distinctly brownish coloration in a considerable part of the zone, overlying a mat of *Vaucheria.* As a rule, however, diatoms are not conspicuous. From October to January the bareness of the zone is usually very striking. Many algae are still represented, but only by isolated threads, which form a thin weft on the surface of the ground, or are only detected by microscopic examination. *Vaucheria* is the most conspicuous alga at this time, often taking possession of large areas. Closer examination may reveal the presence of a few filaments of *Enteromorpha, Rhizoclonium* or *Microcoleus chthonoplastes;* and the diatom *Navicula Grevillii* often forms quite definite films, stabilising the surface of what would otherwise be quite bare mud.

In February *Ulothrix flacca* develops as in zone A and all other forms then become subsidiary. A brown alga may also be present about this time. As before, this phase is short lived and in March *Enteromorpha* increases rapidly in quantity and for several months is the most striking alga. *Enteromorpha* seems to grow like a blanket on top of *Ulothrix,* and if in early April one digs up the *Enteromorpha,* it is often possible to find pure masses of *Ulothrix flacca* underlying it. Sometimes it is found to overlie the brown alga in the same way. *Rhizoclonium* may be present at this stage to a small extent, and *Vaucheria* may occur locally. Towards the end of August *Enteromorpha* begins to decrease in amount, and the zone becomes barer in appearance, the blanket of green alga giving way to patches of a duller hue dominated by Cyanophyceae or diatoms. Quite a number of blue-greens are to be found at this stage. Extensive sheets may occur, some of which can be stripped off from the surface of the ground quite easily. These are dark blue or olive-green to brown in colour, and are caused by a mixture of *Oscillatoria* and *Phormidium* spp. (*Oscillatoria nigro-viridis, O. corallinae, O. Bonnemaisonii, O. laetevirens, Phormidium tenue, P. foveolarum* and *P. angustissimum*). *Spirulina* spp. are also present at times in the films. Other extensive areas may bear blue-greens of a very different macroscopic appearance. Here quite definite streaks can be seen on the surface of the soil with a hand lens, and the algae obviously penetrate the soil much more intimately so that the film does not easily separate from its surface. In such spots *Microcoleus chthonoplastes* is the dominant form, and it is often accompanied by scattered filaments of one

or more of the Cyanophyceae mentioned above. Here and there small well-defined circular colonies of much brighter colour are to be noticed, especially near the moist margins of the zone. These are due to *Anabaena* or *Nodularia*, or to mixtures of the two. Diatoms are frequently present in considerable numbers amongst the Cyanophyceae. *Navicula formosa, Scoliopleura tumida, Amphora lineolata* and *Nitzschia obtusa* are amongst the most important, and species of *Navicula* which form tubes (*Schizonema*) are to be expected. This phase, noteworthy for the prevalence of Cyanophyceae, persists until September or October, when the blue-greens begin to wane, the soil becoming exceedingly bare by November, except perhaps for *Vaucheria*, which is usually present to some extent all the year round, unless erosion is too severe.

C. *Obione zone.*

Owing probably to the dense shrubby nature of the *Obione* plants the algal vegetation of this zone is confined for the most part to thin films in which the diatoms and Cyanophyceae are the most important. The diatom flora does not vary appreciably according to the season of the year in its composition. The dominant forms are apt to differ locally, but they are nearly always small in size. *Navicula Grevillii* is a very common form, and *Nitzschia obtusa* var. *scalpelliformis* often occurs in great abundance. Other diatoms typical of this zone are *Navicula subinflata* var. *elliptica, N. cincta* var. *heufleri, Stauroneis septentrionalis, Gyrosigma Spenceri* and *G. scalproides* var. *eximium.*

The bareness of the zone is most marked in the winter months, November–January, or February, when there is practically nothing except a few diatoms and isolated threads of *Microcoleus chthonoplastes* and *Phormidium autumnale.* Towards early summer, March–June, Chlorophyceae may also occur locally, being represented by a thin weft of *Vaucheria* siphons or strands of *Rhizoclonium* or by some form of *Enteromorpha.*

From July to October Cyanophyceae become very prominent, often covering extensive areas which are overshadowed by the phanerogams, although the larger Chlorophyceae may still persist to some extent in the more open spots. The Cyanophyceae most frequent are *Microcoleus chthonoplastes, Anabaena torulosa, Oscillatoria Bonnemaisonii, O. laetevirens, O. brevis, O. nigroviridis* and *Phormidium autumnale.* Several or all of these algae may occur in the same stratum, the dominant alga varying locally.

Bostrychia scorpioides is present as an epiphyte on the stems of *Obione* at most times of the year.

This zone is separated from the Upper *Glyceria* zone by a steep escarpment. This seems to support a definite alga flora (see later, p. 365).

D. *Aster-Glyceria zone.*

Owing to the matted nature of the phanerogams, which are often beaten down prostrate by the force of the tidal waters, the growth of algae is much interfered with, and usually there is only a filmy growth of Cyanophyceae and

diatoms, with abundant *Enteromorpha* at certain times. The Cyanophyceae and diatoms grow on any exposed soil, or on silt which has been deposited after high tides on the prostrate grasses. After a recent high tide the zone may appear to be exceedingly bare except for *Enteromorpha*.

The diatom flora is very variable and it was not possible on the data available to correlate the variations with changes in the tides. It seems most likely that the variation is merely due to the local distribution of different species. *Gyrosigma Wansbeckii*, *G. scalproides* var. *eximium*, *G. Spenceri*, *G. diaphanum*, *Navicula litoralis*, and especially in the summer months such small forms as *N. cincta* var. *heufleri*, *N. gregaria*, *Nitzschia subtilis* and *N. lanceolata* are the usual diatoms encountered. From late autumn to early spring, October to February, the bareness of the zone is most marked, since, apart from diatoms, little is to be found except a scanty growth of Cyanophyceae such as *Oscillatoria nigro-viridis*, *O. Bonnemaisonii*, or *Phormidium autumnale*. In January and February *Ulothrix flacca* may appear in the lower marginal parts of the zone, and later *Enteromorpha prolifera* appears, increasing in amount, until by June it has become an important constituent. *Enteromorpha minima* is also washed up in large quantities at this time as an epiphyte on drift of various kinds. In July, Cyanophyceae become increasingly important. *Anabaena* and *Oscillatoria sancta* are present in great quantity, the first often forming extensive pure stretches in which there is scarcely anything else. *Microcoleus chthonoplastes* is not rare at this stage. The Cyanophyceae retain their importance during July to September. *Enteromorpha* seems to persist later in the season here than in the lower zones.

E. *Upper Glyceria zone*[1].

The algal vegetation in this zone seems to be most stable all the year round and there is little seasonal variation. The algae include merely diatom or Cyanophyceae films with local patches of a form of *Enteromorpha prolifera*

---

[1] Festucetum and Armerietum zones at Canvey. It has already been stated that when this investigation was nearly completed, it was brought to my notice that areas of salt marsh dominated by *Festuca rubra* L. and *Armeria vulgaris* Willd. respectively are to be found at Canvey, on the north side of the island, and at some distance from the area under investigation (see p. 345). I am very greatly indebted to Dr W. B. Turrill not only for giving me this information, but also for showing me the areas in question. They occur near Pantile Farm and the *Armeria* zone is in a part of the marsh which is very heavily grazed and trodden by cattle, and is therefore not strictly comparable either with the undisturbed area investigated on the other side of the island, or with the Ynyslas marsh which is used for the grazing of sheep. The *Festuca* zone was examined in January, 1930, but the turf was so close and compact that it yielded no algae. The *Armeria* zone was examined in July, 1930. It formed at that time a close sward 6–8 in. high, and *Juncus Gerardi* Loisel formed a large proportion of the turf. *Triglochin maritima* L. is common, but *Limonium vulgare* Mill. and *Spergularia rubra* Pers. are occasional. *Enteromorpha prolifera* and *Bostrychia scorpioides* are the most important algae. The *Enteromorpha* varies from slender filaments in hair-like tangles to broad irregularly inflated and convoluted fronds, all probably variations of the same species (to be described in Part II). Fragments of a sterile *Vaucheria* and of a brown alga belonging to the Ectocarpaceae are also occasional. No Cyanophyceae were seen and very few diatoms.

and *Bostrychia scorpioides* adhering to the base of the grasses. The grasses are so thick that extensive algal growths are not possible. As regards diatoms dominance varies, and there is no sharp seasonal restriction of the species. *Nitzschia obtusa* var. *scalpelliformis*, *Navicula elliptica*, *N. litoralis*, *N. gregaria*, *N. mutica*, *N. heufleri*, *Stauroneis septentrionalis* and *Gyrosigma Spenceri* are the most important forms.

The most important Cyanophyceae are *Phormidium autumnale* and more especially in the autumn months, *Oscillatoria nigro-viridis*, *O. Bonnemaisonii*, *O. brevis* and *Microcoleus chthonoplastes*.

Bostrychia scorpioides and *Enteromorpha* may be found at almost any time of the year.

V. Pans and channels[1].

Pans. Pans at Ynyslas which have no outlet and are full of water all the year round except in long periods of drought usually have no important algal flora with the exception of a layer of algae which encrusts the mud at the margin of the turf. At certain states of the tide, some pans, especially those near the margin of the marsh, may contain considerable quantities of drift material, including many of the larger Phaeophyceae, as well as many Rhodophyceae and also *Enteromorpha*, but it is probable that such algae, even if living when washed up, enjoy only a very short existence on the marsh, since they are often bleached or in an advanced stage of decomposition. The pans at Canvey were usually free from larger algae, but on one occasion in July, a pan showed considerable quantities of free-floating *Enteromorpha* sp., which, upon examination, gave the impression of being merely drift weed, since it included representatives of almost every different form of *Enteromorpha* occurring on the marsh at that time. (The range of variation in this genus will be described in Part II.) It would appear that *Enteromorpha* may persist in such pans for a short time, but, as far as observations go, it is not to be considered as a permanent inhabitant when free floating in pans.

Sometimes in late summer, certain pans with standing water, especially those less disturbed by the tides in the highest parts of the marsh, as for example near the Juncetum at Ynyslas, tend to develop a very conspicuous plankton flora, which at times reaches the extent of a bloom. This was noticed after a long period of warm weather in 1929 at Ynyslas. The dark brownish bloom referred to was in this case caused by *Anabaena torulosa*, forming a thick tenacious bubbling film and producing spores in great quantity. Most of the other pans at this time, however, were quite dry, often with the mud at the bottom showing cracks, or with an incrustation of salt resulting from the evaporation of the brackish contents. Even if water remained in the pans, it showed as a rule only an insignificant pale surface film. Such a scanty bubbling scum was due to large quantities of the tiny diatom *Nitzschiella*

---

[1] See also Part III, Marginal Community of Diatoms..

longissimum and the chrysomonad *Hymenomonas coccolithophora.* Locally a bright brownish coloration of the surface film denoted the presence of a species of *Glenodinium,* which unfortunately encysted before it could be determined. A pale scum taken from a pan at Canvey in June, 1926, showed a considerable diatom flora, in which *Scoliopleura tumida, Amphora proteus, Navicula didyma, N. pygmaea* and *N. gregaria* were the most important forms. *Merismopedia* spp. were not uncommon with the diatoms. These observations made at Canvey and Ynyslas show that the floating flora of pans is liable to local variation.

Pans full of water may further possess a bottom flora recognisable as a blue-green or brownish film on the surface of the mud, or by the evolution of bubbles of oxygen resulting from photosynthesis. This bottom flora, always small in amount, might easily be overlooked. On one occasion at Ynyslas, a fairly definite stratum of *Oscillatoria Bonnemaisonii* was seen covering the mud at the bottom of a full pan, and on another occasion, the bottom mud yielded *Nitzschia rigida, Navicula gregaria, Gyrosigma diaphanum* and other diatoms in fair quantity (July, 1928). A similar pan at Canvey containing no visible algae either floating or on the bottom was examined. Mud and water taken from this pan yielded on standing quantities of *Nitzschiella longissimum* together with *Nitzschia apiculata* and *Navicula cincta* var. *heufleri,* also occasional strands of *Pseudanabaena* and *Nodularia* (August, 1929). Possibly warm favourable weather conditions are essential to the production of this bottom flora.

At Ynyslas the margins of the pan seem to be, in contrast to the standing water, a very favourable habitat for the growth of algae, and, except when the swirling of the water in the pans during high tides causes the erosion of the marginal soil, a covering of encrusting algae is nearly always found there. *Rivularia* is a very important form, and the margins of most pans are studded with its tiny hard colonies, except in the drought of summer, when a whitish incrustation seems to obscure the usually dark colonies (see also Part II). Species of *Phormidium* and *Lyngbya* may accompany the *Rivularia,* and, further, *Microcoleus chthonoplastes* and *Lyngbya aestuarii* are also to be found at times taking part in the encrusting flora of the pan margin. Where such a community of Cyanophyceae does not occur, *Rhizoclonium* or *Enteromorpha percursa* are very common forms, apparently spreading from the adjoining turf. *Rhizoclonium* is much more frequent than *Enteromorpha,* and often covers large areas at the margins. Under favourable conditions, as, for example, in the case of a small pan near the margin of the marsh which had been drained of standing water, but was still moist, *Rhizoclonium* covered the whole surface of the bottom of the pan. Usually, however, it only encrusts the margin or floats as delicate tufts from the sides into any standing water which may remain in the pan. The presence of algae at the margins of pans is further dependent on favourable climatic and tide conditions, so that after a stormy period with high tides the margins of the pans even at Ynyslas may show

signs of erosion and be practically free from algae. The marginal flora of the pans at Ynyslas is thus related partly to the escarpment community (see p. 363) and is further enriched by the invasion of algae from the adjoining turf.

This marginal flora is not developed in the same way at Canvey, and in consequence the pans are usually very bare. This may possibly be due to the fact that they all lie in the Upper *Glyceria* zone, which does not possess such a conspicuous alga flora as the Armerietum and Lower Festucetum at Ynyslas, in which zones the pans mostly lie in the case of the Welsh marsh. At Canvey, thick mats of grasses surround the margins of the pans so that cryptogams would be crowded out even if there were a copious alga flora in the Upper *Glyceria* zone from which they could spread. The submerged parts of these grasses in pans with standing water frequently become festooned, however, with a copious growth of filamentous diatoms, such as *Melosira* or *Navicula* spp.

Drying and colonising pans[1]. Pans which have only recently become dry, as for example in dry weather associated with periods of non-disturbance by tides, do not usually possess any striking alga flora. The surface, frequently cracked, usually reveals, on examination, little more than a few diatom frustules, which, more often than not, are dead and empty. Locally, as already described in the case of a pan at Ynyslas, favourable conditions may induce *Rhizoclonium* or *Lyngbya aestuarii*, which are abundant in the adjoining turf, to invade the drying mud of the pan and to cover considerable areas. This, however, only happens in exceptional conditions and the occurrence of these forms does not necessarily denote that silting of the pan is in progress or that phanerogams will appear. Such colonisation is probably only transient and the algae will disappear with less favourable conditions.

If a pan is really silting up, however, owing to efficient drainage, so that it will in time be suited to the growth of phanerogams, a conspicuous alga flora will first be developed, preceding its colonisation by *Salicornia*. At Canvey the succession of algae in such silting pans is very similar to the colonisation of the hummocks of slightly higher level in the wider channels (see p. 355). A particular example of a silting pan was studied at Canvey on the north side of Benfleet Creek near Benfleet and about two miles away from the locality of the main investigation. Here pans showing obvious silting were observed, the level of the bottom being obviously higher at one end than the other. Samples of the surface mud taken furthest from the silting area in such a pan, showed only a very sparse flora of fragmentary *Oscillatoria corallinae* or a few diatoms such as *Scoliopleura tumida*. Where silting was just starting *Oscillatoria sancta* and *Microcoleus chthonoplastes* were present in addition, and diatoms were more abundant. Very slender species of *Phormidium* may also occur, as well as *Spirulina* spp. and *Nodularia*. *Vaucheria* is an early coloniser in silting pans, but it seems to succeed the Cyanophyceae. It is present, however, in some quantity and can be seen to penetrate the soil of the pan to considerable

[1] See Yapp (4), p. 95.

depths long before *Salicornia* establishes itself. The habit of the alga doubtless renders it particularly important in silting areas (see also Part II).

A study of similar silting pans at Ynyslas also shows that Cyanophyceae are the first colonisers, apart from diatoms. Examination showed that furthest from the silting area there was a stratum of Cyanophyceae in which *Oscillatoria corallinae* was dominant, with *Microcoleus chthonoplastes*, *Lyngbya aestuarii* and *Oscillatoria Bonnemaisonii* in the given order of frequency. Where silting had been in progress for a little longer, *Microcoleus* became more abundant, otherwise the mixture was much the same. In areas still more silted, however, there were obviously green algae, and here *Rhizoclonium* was dominant, whilst *Lyngbya aestuarii* was very common. *Nodularia* and *Vaucheria* were also present here. In another pan at Ynyslas which had reached the *Glyceria maritima* stage as regards phanerogam colonisation, *Vaucheria* was the dominant alga, and associated with it were *Microcoleus chthonoplastes* and *Lyngbya aestuarii*. It would seem probable, therefore, that at Ynyslas *Rhizoclonium* is the first green alga to appear, *Vaucheria* following later, whereas at Canvey the *Rhizoclonium* stage is omitted. This can be correlated with the fact that *Rhizoclonium* is of relative unimportance in the alga flora at Canvey, whereas it occurs in great abundance at Ynyslas.

Channels. Channels are frequently quite bare, except for their upper margins which are sheltered by overhanging phanerogams and are less subject to disturbance by tides, and excepting also the film of diatoms which is usually present on the surface of the soft mud at the bottom. The frequent filling up of the channels by the inflowing tide apparently keeps them unvegetated. At the same time the channel is quite a favourable habitat for the growth of algae, and in July, 1929, following a long period of drought at Ynyslas, when most of the grassy turf was so parched and dry that it yielded almost no recognisable algae, the sides of some of the larger channels were abundantly clothed with algae, which flourished in the moister and more sheltered substratum there in spite of the unfavourable weather conditions.

Vaucheria is a very frequent form in the soft mud at the sides of channels, and its dark velvety pile often covers considerable areas. *Rhizoclonium*, *Enteromorpha* spp. and a representative of the Ectocarpaceae are less frequent inhabitants. In the appropriate season, *Anabaena* may produce its large bright blue-green shining colonies (July, 1929).

VI. ESCARPMENTS.

The escarpments at Ynyslas are usually the result of erosion by tidal waters. They are marginal, or may be located further back in the marsh owing to Secondary Marsh formation at the base of an original marginal escarpment (see Yapp, **4**, p. 82). These vertical escarpments usually cut into the Armerietum, Lower or Upper Festucetum, and sometimes there is also a vertical escarpment between the Juncetum and the adjoining turf. The richness of the flora

of these vertical faces depends on the length of time which has elapsed since the escarpment was formed, and especially in the case of marginal escarpments on whether there has recently been erosion by tidal water, which may result in the annihilation of the forms which had succeeded in establishing themselves. Ordinary neap tides do not seriously interfere with the vegetation of the marginal escarpments as observations on this marsh show, but in times of storms or very high tides the surface of the escarpments may be largely denuded. During the period of these investigations the most violent erosion of the marginal escarpments was observed to take place in mid-winter (January) and mid-summer (July).

The most constant and conspicuous form inhabiting all escarpments, both marginal and further back in the marsh is *Rivularia*. Its small, hard, black colonies are to be found at all times of the year closely scattered on all vertical surfaces, including the margins of pans. It becomes most conspicuous in the wet winter months, at which time it may invade the turf, extending horizontally from the top of the escarpment. In dry conditions, especially after long rainless periods in summer, it may become quite inconspicuous, or be obscured by a white incrustation as in the case of the margins of pans.

The tiny interstices of soil between the *Rivularia* colonies are usually covered with species of *Phormidium*, such as *Phormidium autumnale* or *Phormidium molle*. With these is also a species of *Endoderma*, and *Phaeococcus* is also frequent at times. This association of algae is quite general on escarpments which have not recently been disturbed. The diatom *Navicula Grevillii* is frequently encountered in all samples taken from vertical faces and is probably the first settler on all escarpments newly eroded (see p. 366). All the above algae are particularly suited to the environment in which they are usually found. The close growth of tough *Rivularia* colonies and tightly interwoven *Phormidium* filaments frequently form a continuous sheet over the surface of the escarpment which must be of very great assistance in protecting its surface during submergence at times of spring tides. The toughness of a stratum of *Navicula Grevillii* is very striking. It is very difficult to separate the filaments from the soil particles and the resistance to tidal action must be very great (see also Part II). The *Rivularia* colonies adhere very closely to the surface of the soil, so that, in general, the escarpment is firmly cemented by these surface algae.

Besides these algae which are especially characteristic of escarpments, large stretches of the vertical faces may be covered, when conditions are suitable, with other algae, which in the presence of sufficient moisture, spread from the adjoining turf. This is especially the case with the marginal escarpments. *Rhizoclonium* often spreads in this way, and especially in August–May, large areas of the marginal escarpment may bear a green blanket of pure *Rhizoclonium*. Rarely *Enteromorpha percursa* may occur locally. In the spring months, March–May, filaments of *Ulothrix* spp. and masses of *Pylaiella litoralis* may adhere to the bare mud. *Ulothrix* is always small in amount and

is usually mixed with other forms. Various forms of *Enteromorpha prolifera* may sometimes be found on the escarpments, including, as one would expect, the forms which are to be found in the loose weed of the Salicornetum and Glycerietum. In addition, however, local growths of the curled and crisped form commonly found at Canvey (*Glyceria* zone) are present (cf. B. IV, Part II), and *E. compressa* also occurs in some quantity.

These larger Chlorophyceae, *Rhizoclonium* and *Enteromorpha*, seem to be of more superficial growth than the Cyanophyceae and tubular diatoms, and the blanket which they form always separates quite easily from the soil. Thus, whilst they must, when present, protect the surface of the soil to some extent, it is likely that they will be fairly easily washed away, and will not be so resistant as the smaller algae which penetrate the surface layers of the soil much more intimately. Moreover they are less permanent colonisers, being more dependent on moisture than the diatoms and blue-greens.

At Canvey, as at Ynyslas, the different zones are frequently separated from each other by small escarpments, but these are never as deep as in the Welsh marsh. The most constant escarpment is that between the *Aster-Salicornia* zone and the bare mud of the channel. This seems to have no special flora such as the escarpments at Ynyslas possess. Its vegetation has already been described (see p. 356). The escarpment between the *Obione* zone and the Upper *Glyceria* zone in Area No. 2 at Canvey seems, however, to show some resemblances to the escarpment flora at Ynyslas. *Rivularia* does not occur here, but *Endoderma*, *Navicula Grevillii* and *Phaeococcus* are quite typical forms. *Oscillatoria brevis* is also quite common, but *Phormidium autumnale* is by far the most important alga present, giving a definite blue-green colour to the firm surface of the escarpment. Chlorophyceae never play any important part in the vegetation of this soil, possibly because the adjoining Upper *Glyceria* zone is not as rich in these algae as the turf of the Welsh marsh. Thus the blankets of *Rhizoclonium* so frequently seen on the escarpments at Ynyslas are entirely wanting, whilst *Vaucheria* and *Endoderma* are rare and are not often present in sufficient abundance to give a distinct coloration to the soil. The entire absence of *Rivularia* is perhaps the most striking fact.

VII. PIONEER ALGAE.

At Ynyslas algae do not seem to play any important part in the stabilising of the marginal silt. Amongst the *Salicornia* plants only superficial tufts of *Enteromorpha* are to be found; these do not penetrate into the mud and could only be very subsidiary in stabilising the shifting soil. The diatoms also presumably cannot do much in promoting colonisation, and it is only very rarely in autumn that Cyanophyceae are present in sufficient quantity to form a continuous sheet. As a rule they are only present as isolated filaments buried in the sand. The probability is, therefore, that algae play a very insignificant part in stabilising the open mud at Ynyslas.

In the case of the vertical escarpments, however, algae are probably more important. This has already been referred to (see p. 364). With the object of discovering which algae are the first to take possession of newly bared soil, part of a vertical escarpment rising steeply from Glycerietum to Armerietum was denuded of all algae in September, 1927. The surrounding untouched soil bore *Rivularia*, *Phormidium* and *Navicula Grevillii*, etc. It was found in November, 1927, that only a few threads of *N. Grevillii* had succeeded in establishing themselves on the bare soil. Nevertheless these had performed a rather remarkable feat in obtaining a foothold at that time, since at the end of the previous month one of the most severe storms experienced for many years, associated with an unusually high tide, occurred along that coast. In January, 1928, the stratum of *N. Grevillii* was much denser, and amongst the threads were filaments of *Phormidium autumnale* and *Endoderma*. At a much later date *Rivularia* appeared.

At Canvey the soft tenacious mud offered far more opportunity for colonisation than the more shifting sandy soil in the estuary of the Dovey, and the wide channels with their extensive stretches of mud frequently showed mounds which were obviously of higher level than the surrounding mud (see Fig. 1). These were in various stages of colonisation. The oldest already bore phanerogams, those bearing only *Salicornia* being younger than those which supported both *Aster* and *Salicornia*. The youngest hummocks bore only algae.

Young hummocks not yet bearing phanerogams were examined at various times from October, 1926, and were found to possess a flora of Cyanophyceae in which *Oscillatoria corallinae*, *O. sancta*, *Phormidium foveolarum*, *P. angustissimum* and *Microcoleus chthonoplastes* were abundant. Diatoms such as *Navicula Grevillii*[1], *Gyrosigma scalproides* var. *eximium* and *G. Spenceri* were numerous, as well as occasional specimens of any of the usual marginal forms. The stratum of blue-greens, in which *Oscillatoria* spp. and *Phormidium* spp. are the chief forms is a superficial sheet which does not penetrate the mud very much, but which, being continuous, firm and tenacious must form a protective layer which would prevent the silt being washed away unless there were a very strong current. If there is any considerable amount of *Microcoleus chthonoplastes* present, however, the stratum must be of much greater importance, for this alga has great penetrating capacity, and its living trichomes, as well as its persistent empty sheaths, can be distinguished at a depth of 1–5 mm. below the surface of the ground. These threads of *M. chthonoplastes* penetrate the soft mud in all directions and help to make it firm. Examination of soil bearing a film in which only *Oscillatoria* spp. and *Phormidium* spp. occur, showed that at a depth of 1 mm. beneath the surface of the soil merely fragments of these algae could be found, and it was only very rarely that any trace of them could be found at a lower level.

Whilst these Cyanophyceae seem to be early colonisers on rising hummocks,

---

[1] See also Part II.

Vaucheria becomes very prominent at a slightly later stage. It may be abundant even before phanerogams have established themselves, and it is a very important constituent on hummocks which already bear *Salicornia*. *Vaucheria* must be a very efficient collector and binder of silt, since its filaments branch and penetrate the mud in such a way that it is almost impossible to wash the alga free from soil particles (see also Part II). In addition to these filaments penetrating the mud, soil clothed with *Vaucheria* also shows a velvety growth of upright filaments which must serve to collect silt during flooding by high tides. When both *Microcoleus* and *Vaucheria* are established, the hummock is very well protected from the force of all ordinary tides, for the surface soil to a depth of 5–10 mm. is rendered tough and gelatinous in consistency by the penetrating algal filaments. *Oscillatoria* spp. and *Phormidium* spp. persist in quite old hummocks.

When extreme drought coincides with the incidence of neap tides, the loss of water from the surface of the mud in the channels may cause considerable contraction of the superficial layers. Such conditions prevailed in May, 1927, with the result that the surface of the open mud became cracked with narrow fissures which doubtless render the mud much more vulnerable to the eroding action of succeeding high tides. The protective value of *Vaucheria* was then quite obvious. Hummocks which had been colonised by this alga previous to the drought, showed no such fissures as the bare mud. The substratum, although quite unbroken, showed a peculiar honeycomb appearance. This proved to be due to the presence of anastomosing ridges projecting from the surface, about 2 mm. in height and enclosing areas 5–15 mm. in diameter. Both walls and floor of these shallow "cells" were composed of *Vaucheria* filaments in poor condition; Cyanophyceae, represented by any of the above-mentioned forms, were also present, though chiefly in the floors. The drought, therefore, instead of causing the cracking of the soil, merely resulted, in these areas where algae had established themselves, in the drying and contraction of the surface material, the erect siphons of *Vaucheria* being drawn together in drying to form the raised ridges on the surface. The soil itself, permeated in all directions by the *Vaucheria* siphons and tubes of *Microcoleus chthonoplastes*, is well protected and does not crack. The algal filaments ramifying in the soil probably prevent cracking by giving mechanical strength as well as by conserving moisture by virtue of their colloidal nature.

VIII. SOME OBSERVATIONS ON TIDAL EFFECTS.

These observations are necessarily very incomplete. It was recognised by the writer that the frequency of submergence by high tides and the varying periods of desiccation in the different zones owing to non-submergence must have an effect on the algae, and each species, if studied, would probably show some correlation in its occurrence with the tidal conditions in each zone. Each

species would have to be investigated individually, however, and this has not been attempted. The following general observations on tidal effects may, however, be of some value.

Neap tides do not flow up as far as the *Salicornia* zone. This is true both at Ynyslas (see Yapp, **4**, p. 74) and at Canvey. In the latter region it was observed on August 27th, 1928, that the tide rose to its highest and receded again without reaching the phanerogam zones. This was 10 days after the previous spring tide and 6 days before the next expected one. From this it seems probable that the lowest phanerogam zones are not submerged on more than 8 or 9 days in a month and the upper zones for a much shorter period.

The effect of higher tides was studied at Canvey on July 8th, 1929, when a spring tide was expected. The tide was observed to run in very quickly and also to recede very quickly, all the phanerogams being covered and un-covered again in less than 2 hours. The water was very turbid and muddy, although the weather was quite calm, and the margin of the advancing water bore a whitish foam. This foam or scum was examined and found to contain a fair proportion of dead and living diatom frustules. Similar foam was also seen on the Ynyslas marsh on May 5th, 1928, when a distinct line of it was deposited about half way through the Armerietum zone. Examination in this case revealed nothing but minute soil particles. This is not surprising as the diatom flora at Ynyslas is considerably poorer than that of Canvey.

On July 8th, 1929, the Upper *Glyceria* zone at Canvey was completely covered, and subsequent observations showed that the *Glyceria* plants were wet to a height of 3 in. from their base, so that the water had risen to about that level. At Ynyslas ordinary spring tides just cover the Lower Festucetum (Yapp, **4**, p. 74). These observations tend to show that the Juncetum and Upper Festucetum zones occurring at Ynyslas have no equivalent at Canvey in the area investigated. Prof. Yapp had often expressed surprise that *Glyceria*, which is a pioneer plant at Ynyslas, should be the dominant con-stituent of the uppermost zone at Canvey. The above observations show, however, that in relation to the tides, the plant occupies an equivalent position in level in both marshes.

The effect of high tides at Canvey is to deposit a visible layer of mud all over the marsh. This is most conspicuous in zones where *Glyceria* is dominant. In this zone also submergence seems to wash the grasses flat, quantities of it lying bent and prostrate, so that the surface of the soil is completely covered, and it is necessary to raise the wet haulms in order to expose the soil. On top of the prostrate grasses, a layer of fine silt is deposited. This is the condition in both the *Aster-Glyceria* and Upper *Glyceria* zones. The algal flora of these zones is very sparse at such times as far as diatoms and small algae are con-cerned. The effect of the tide is to bury the existing algae under a layer of silt, and apparently they do not have time, between morning and evening high water to collect on the surface of the silt in response to light. This is apparent

since there was no appreciable difference in the number of algae obtained from samples taken from the surface silt before and after submergence by the tidal waters. Of course, if masses of *Enteromorpha* are present in these two zones, as is frequently the case, the amount of silt deposited at the time of spring tides is not sufficient to bury these larger algae, but there is usually a visible deposit of mud all over them.

More silt seems to be deposited in the *Aster-Glyceria* and Upper *Glyceria* zones than elsewhere on the marsh, probably owing to the filtering action of the thick grasses. In the *Aster-Salicornia* zone the *Enteromorpha* blanket was covered with a visible deposit of mud. In the channels, where bright blue-green films of Cyanophyceae were conspicuous, very little decrease in the brilliance of the colouring was noticed after the tide had submerged the area and then retreated, since very little silt seemed to have been deposited there.

At Ynyslas, the conditions indicated seem to be a gentler current, which, however, because of the looser and more sandy substratum, results in relatively greater erosion than in the Canvey marsh. Because of the difference in the nature of the soil, the tidal water is less muddy, and there is not the same conspicuous deposit of silt to be seen on the vegetation after a high tide. Only by the line of drift algae or debris, and the moister nature of the vegetation to the seaward side of the drift line, could it be recognised that the tide had ascended and then receded. It would further seem that many of the ordinary spring tides do not reach up as far as the Lower Festucetum, since the line of drift at expected spring tide often lay in the middle of the Armerietum or lower. The effect of the tides in continually churning up the loose sandy soil of the estuary and washing it into the colonising *Glyceria* zone is probably to prevent the algae from establishing themselves easily in that region (p. 349). This results in the comparative barrenness of this zone as compared with the marginal *Aster-Salicornia* zone at Canvey.

Large quantities of drift weed are deposited at times on the marsh at Ynyslas. This drift may include, besides *Enteromorpha*, large masses of Fuci, *Laminaria*, *Chorda filum*, and various Rhodophyceae. This drift weed invariably decays where it is deposited, often causing the bleaching of the under-lying grass when it has been thrown up as high as the turf zones. In addition to these large masses of drift weed the frequent occurrence of ropes of living Chlorophyceae, largely *Rhizoclonium*, which lie on the turf in the Glycerietum or Armerietum zones, or hang suspended from the escarpments, have already been referred to (p. 349). Cotton (2), also noted the occurrence of such ropes on the salt marsh near Clare Island.

At Canvey, although there is a far more copious development of algae at the margins of the marsh than at Ynyslas, algae do not feature in the drift deposited here after high tides. *Enteromorpha minima*, which is abundant as an epiphyte, is often thrown up as drift still attached to its substratum of larger algae or debris, but the more abundant species of the genus, *E. prolifera*,

is rarely found as drift. Certainly one never finds ropes of algae such as occur so frequently at Ynyslas. *Porphyra*, however, is deposited at times at the margins of this marsh.

A peculiar phenomenon was noticed on the Ynyslas marsh in November, 1927. The marsh was visited about 10 days after the storm of October, 1927, when strong winds coinciding with a very high spring tide, resulted in the tidal waters rising to an unusual height, so that the Dovey valley was flooded, causing much damage and destroying many hundreds of sheep in the surrounding fields. When the marsh was visited it was still very wet, and the escarpments at the margins of the marsh showed signs of severe erosion. *Rivularia* seemed capable of withstanding the severity of the storm very well, and many exposed parts of escarpments covered by its colonies were intact. The pans were full to the brim, and there were signs of their having been overfull for some time, since at a little distance from the margin of each was a light brown deposit of fine mud on the turf, as if this had settled from the water when the pan was overfull, and had been left behind when the level of the water in the pan fell. This brown deposit round nearly every pan was found to consist of almost pure *Gyrosigma Spenceri*, with some *Pleurosigma angulatum* and *Navicula gregaria*, and very occasional other diatoms. There was no appreciable amount of inorganic silt in the deposit, which consisted of almost pure living diatom frustules. This proof of the capacity of diatoms to flourish and multiply in the cold months of the year was very striking.

REFERENCES.

(1) **Bracher, R.** "The ecology of the Avon banks at Bristol." This JOURN. **17**, 35, 1929.

(2) **Cotton, A. D.** "Clare Island Survey 15, Marine Algae." *Proc. Roy. Irish Acad.* **31**, 1912.

(3) **Marsh, A. S.** "The marine ecology of Holme-next-the-Sea, Norfolk." This JOURN. **3**, 1915.

(4) **Yapp, R. H., Jones, O. T.** and **Johns, D.** "The salt marshes of the Dovey Estuary." This JOURN. **5**, 1917.

(To be continued.)

A BIRD CENSUS ON LUNDY ISLAND (1930)

By V. C. WYNNE-EDWARDS and T. H. HARRISSON.
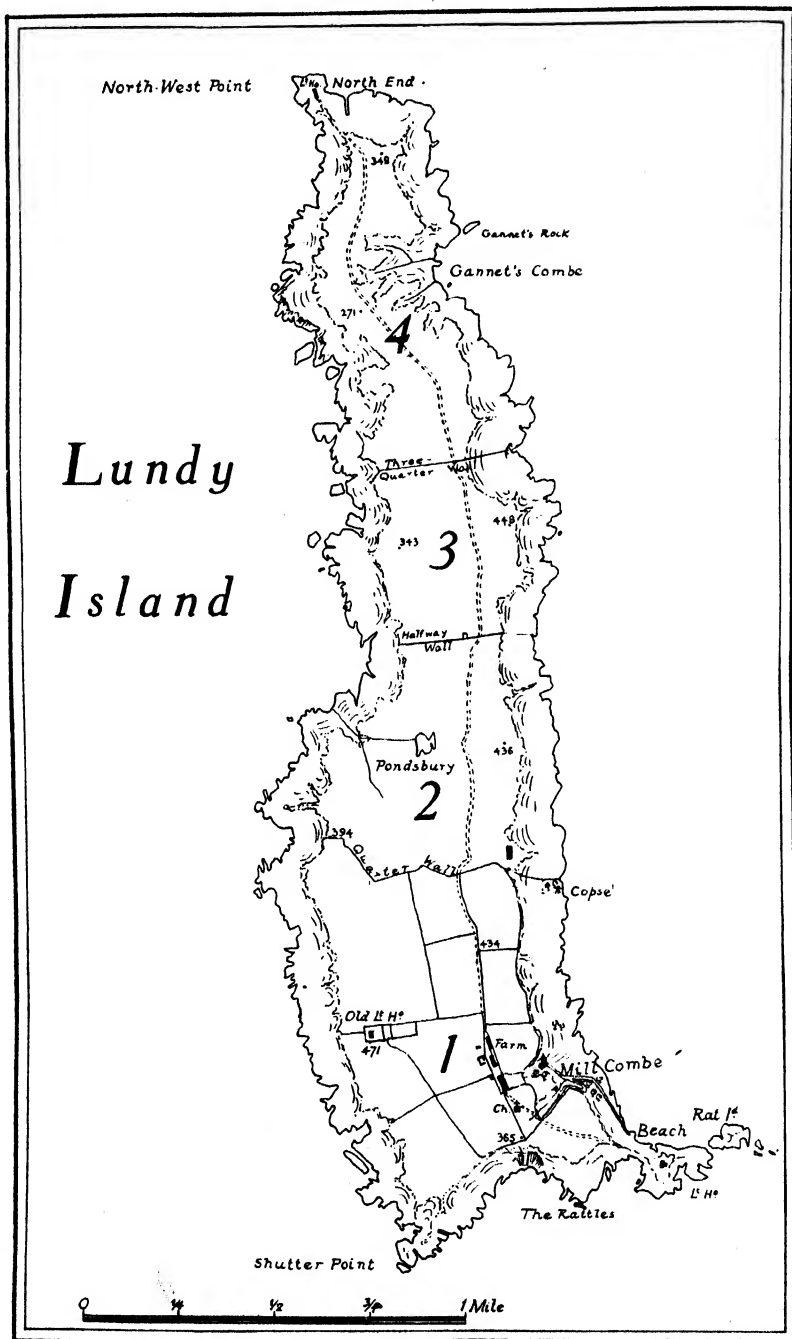
(*With one Map in the Text.*)

AN island is well suited for bird-census work because it is a natural entity. If it is far enough from the mainland and other islands there is no interchange of birds between the census area and those adjacent to it, and thus the numbers obtained for the various species are the actual numbers supported on the census area, because there is nowhere else for the birds to feed.

Lundy lies in the mouth of the Bristol Channel, 11 miles distant from Hartland Point on the north Devon coast. We were able to establish the fact that rooks and jackdaws do actually make the passage twice daily to feed on Lundy, and very probably the two pairs of peregrines resident on the island sometimes go over to hunt on the mainland. With these exceptions, however, the insulation of the land-feeding birds is probably complete.

The area of the island given by the Ordnance Survey is 1116 acres. It takes the form of an elevated plateau shelving steeply to the sea along its edges; it is roughly 3 miles long, and the breadth increases from about 800 yards at the north end to about 1200 yards at the south. Except for a small area of limestone in the south-east corner the island is granitic, and has much of the character of the Land's End coast. It is divided into four parts by three transverse walls called the Quarter, Halfway, and Three-Quarter Walls. The southern part (Section 1) is rather larger than the others and contains all the inhabited dwellings except one lighthouse.

(a) *Vegetation.* In Section 1 one or two fields are under cereal crops each year; the rest is meadow and pasture land. On the west side of the track in Section 3 there is also an area of grass. The remainder of the island is rough moorland pasture, with small patches of bog and a few small pools, and with a dominant flora of ling (*Calluna vulgaris*), bracken (*Pteris aquilina*), gorse (*Ulex europaeus* or *gallii*), brambles (*Rubus* spp.) and *Salix repens*. This is a "climax" type of vegetation, being stable and not subject to progressive changes.

In each section the plateau or "top" is sharply marked off from the sides (see map). The former is undulating, generally higher on the eastern (leeward) side, and reaching an altitude of 471 ft. at the Old Lighthouse. The sides are exceedingly rugged, broken by huge crags, and ending below in an almost continuous precipice. The western side is more rugged than the eastern, more exposed to the prevalent winds, and consequently with no cover for small birds in the way of bramble thickets and bushes. The vegetation is stunted,

North·West Point   · North End ·

Gannet's Rock

Gannet's Combe

Lundy

4

271

Island

Three Quarter Wall

343

3

448

Halfway Wall

Pondsbury

436

2

394

Quarter Wall

Copse

434

Old Lt Hᵒ

471

1

Farm

Mill Combe

Chᵒ

Rat Iᵈ

365

Beach

Lt Hᵒ

The Rattles

Shutter Point

0   ¼   ½   ¾   1 Mile

V.C.W.E.

Map of Lundy Island, drawn partly from the Ordnance Survey, by permission.

and along the upper part where it is much cropped by rabbits, the dominant plant is thrift (*Armeria maritima*).

The eastern side is comparatively sheltered, and provides a well-known anchorage off-shore. Most of it is covered with bracken and brambles, but in Section 1 there are a number of well-grown trees, besides a considerable area of planted rhododendrons. There is a small copse by the Quarter Wall composed of old coniferous and deciduous trees. Mill Combe, however, is the most sheltered part of the island; here about 5 acres are well wooded with oaks as well as fir trees, in which the Starlings roost in winter. The farm buildings are also in Section 1. In Section 2 there are some disused quarries on the eastern slope which shelter tall willows and thorn trees. In the northern half of the island there are no trees whatever, but in Gannet's Combe there are many large tussocks of *Carex paniculata* and brambles where willow warblers, whitethroats, song thrushes, blackbirds, hedge sparrows and wrens are found.

The flora of the south-east point is rather different from the remainder. Here samphire (*Crithmum maritimum*) and *Anthyllis vulneraria* are abundant. In passing it may be mentioned that a rough list of eighty-one species of plants was drawn up on the last day of our visit. This is far from complete, and contains only one species of botanical interest, namely *Scrophularia Scorodonia*.

(b) *Fauna.* The fauna of Lundy has been studied by several naturalists. We are indebted to Charles Elton for much of the information which follows. Rabbits are exceptionally abundant, and form the chief food of the buzzards. The black form is common (1930). Puffins nest in the rabbit warren at the north end, some of the burrows still being tenanted by their proper owners. It appears that up to 1926 black rats were very numerous and did considerable damage to the eggs and young of sea birds, but owing to extensive trapping and shooting they have now become scarce. There are no voles of any kind. With the exception of the pigmy shrew, which is quite common at the north end, there are no insectivores on the island. There are no reptiles or Amphibia.

The domestic animals are sheep, cattle and deer. The latter have a considerable effect on the vegetation of the eastern slope, which is covered by a network of their trails.

The insects have been studied by Joy, Donisthorpe, Tomlin and others, and in general differ little from those in similar habitats on the mainland.

THE CENSUS.

The census described here was made between June 7th and 11th, 1930, by the authors and J. H. Comyns. It is confined to the land- and shore-feeding birds. The sea birds are practically independent of the island for their food, and exist in such numbers as to make a census impossible in the case of the herring gull, kittiwake, guillemot, razorbill, puffin and Manx shearwater. T. H. H., however, collected a good deal of data on the numbers of the less

abundant marine species, i.e. greater and lesser black-backed gulls, shag and cormorant, these being represented by fifty, forty-five, thirty and five pairs respectively.

In 1922 L. R. W. Loyd stayed some weeks on the island in May and June and was able to estimate the numbers of several species with accuracy, although no actual census was taken. Loyd's figures (6) are given after our own in Table I, and it is instructive to notice the changes which have taken place since that time.

Table I. *Census of land-feeding birds.*

Species		Sect. 1	Sect. 2	Sect. 3	Sect. 4	Total (1930)	Loyd's figures (1922)
				Number of pairs breeding			
Raven	*Corvus c. corax*	2	1	.	1	4	4 (5?)
Carrion crow	*Corvus c. corone*			T. H. H. estimates		16	6
Magpie	*Pica p. pica*	½	.	.	.	½	0
Linnet	*Carduelis c. cannabina*	28	7	.	3	38	.
Chaffinch	*Fringilla c. coelebs*	6	1	.	.	7	8
House sparrow	*Passer d. domesticus*	21	1	.	.	22	5
Skylark	*Alauda a. arvensis*	17	10	4	8	39	.
Meadow pipit	*Anthus pratensis*	75	105	45	50	275	.
Rock pipit	*Anthus s. petrosus*	19	5	5	12	41	.
Yellow wagtail	*Motacilla f. rayi*	1	.	.	.	1	.
Pied wagtail	*Motacilla a. yarrellii*	4	2	.	.	6	.
Willow warbler	*Phylloscopus t. trochilus*	2	1	.	1	4	0
Blackcap	*Sylvia a. atracapilla*	1	.	.	.	1	0
Whitethroat	*Sylvia c. communis*	3	4	1	2	10	.
Sedge warbler	*Acrocephalus schoenobaenus*	(½)	.	.	.	½	0
Song thrush	*Turdus p. clarkei*	6	2	.	1	9	4–5
Blackbird	*Turdus m. merula*	18	10	3	3	34	.
Wheatear	*Oenanthe oe. oenanthe*	(8)	(2)	(1)	(1)	(12)	4–5
Stonechat	*Saxicola t. hibernans*	7	9	4	8	28	c. 20
Robin	*Erithacus r. melophilus*	7	2	.	.	9	.
Hedge sparrow	*Prunella m. occidentalis*	13	5	1	4	23	2
Wren	*Troglodytes t. troglodytes*	4	5	1	1	11	.
Swallow	*Hirundo r. rustica*	(9)	1	(2)	(1)	(12 +) 1	1
Martin	*Delichon u. urbica*	(6)	(1)	(1)	.	(8)	0
Sand martin	*Riparia r. riparia*	(2)	(1)	(1)	.	(4)	0
Swift	*Apus a. apus*	(3)	(2)	.	.	(5)	0
Cuckoo	*Cuculus c. canorus*	1	.	.	.	1	.
Peregrine	*Falco p. peregrinus*	.	1	.	1	2	1–2
Kestrel	*Falco t. tinnunculus*	1	1	.	.	2	2
Buzzard	*Buteo b. buteo*	2	1	.	1	4	2 (3?)
Wood pigeon	*Columba p. palumbus*	1	1	.	.	2	.
Lapwing	*Vanellus vanellus*	.	3	.	.	3	0
Oyster-catcher	*Haematopus o. ostralegus*	3	4	3	4	14	15
Snipe	*Capella g. gallinago*	.	.	1	.	1	.
Pheasant	*Phasianus colchicus*	3	2	.	.	5	2
					Total...	c. 630	

Note. Some of the birds included in the figures in parenthesis were probably on passage.

We made our census by walking over the whole island in line, noting every male bird in the dimorphic species and every pair of singing birds in other cases—a method which makes no allowance for non-breeding birds. The slopes could be worked in a single sweep, but the top required walking to and fro for a number of times. Under these circumstances some overlapping was inevitable, so that the figure given for the abundant meadow pipit can be

regarded only as a very careful estimate. The four sections were kept separate; Section 1 was surveyed on June 8th, Sections 2 and 3 on the 9th and Section 4 on the 10th. The whole census took just over 30 hours to make. We think the area was adequately covered with the exception of Rat Island, which we did not visit.

The buzzards and carrion crows cross the island so freely that unless their nests are located it is not possible to be sure of their numbers. On any future visit we shall set aside a whole day for this purpose. We met with no difficulty from the presence of young birds. The only species with flying young at the time of our visit were the raven, carrion crow, song thrush, blackbird, stone-chat and lapwing. Conditions were about two weeks behind those on the mainland.

The outstanding difficulty with which we had to contend was the presence of passage migrants. Swallows, martins, sand martins and swifts were plentiful during our visit; only one pair of swallows was proved to be breeding, though we suspect that representatives of all the other species nested in the cliffs (and especially on the limestone area). Some individuals, however, were probably on passage, both of the species mentioned and of the wheatears. A single turtle dove and a wood sandpiper were certainly on migration.

Density of population.

The total number of pairs of land birds (thirty-three species) breeding on the island in 1930 is about 630, of which 90 per cent. are passerines, over 50 per cent. pipits, less than 2 per cent. predaceous birds, and only 9 per cent. summer migrants[1].

The predominance of ground-nesting, and the almost complete absence of tree-nesting species, is self-explanatory.

Excluding islands and rocks lying off the coast, which we did not visit, the area of the whole island is around 1000 acres, of which the "top" occupies

---

[1] *Birds per acre.* The approximate total density of all species works out at slightly more than 1 adult bird to one acre. This figure appears to be low when compared with the very scanty summer data available for other areas in Britain.

The only other complete summer census figures are as below:

Ringwood, Hants. (concentrated island site) 21 adults per acre (5),
Haslemere, Surrey   7·25 ,,   ,,   (8).

A census of summer migrants only, for two areas in Kent (1), gave a density of about 0·6 per acre, which is much greater than that of summer migrants on Lundy.

The average density found by the United States Biological Survey (3) for typical farms in north-eastern America is 2·38 birds per acre, about double the Lundy density. In Illinois, however, Forbes (4) records a density of about 0·9; but figures obtained by Burns (2) in Chester County (U.S.A.) give nearly 2 per acre. Moreau (7) records a maximum density of about 3 adults to the acre on an area in Tanganyika Territory [T. H. H.].

600 and the sides 400 acres. In Section 1, 150 acres of the top are grassland or under crops. The areas of the sections are as follows:

Section	Area of	
	Top (acres)	Whole (acres)
1	247	396
2	156	207
3	89	150
4	114	246

These figures are only approximate, obtained by "counting the squares" at 6 in. to the mile.

It will be seen from the following analysis that those species which are plentiful in nearly every part of the island have a comparatively uniform distribution in the different sections.

Table II. *Skylark.*

	Section				
	1	2	3	4	Total
Area of top (acres)[1]	247	156	89	114	606
Number of pairs	17	10	4	8	39
Density (acres per pair)	14·5	15·6	22·3	14·3	15·5

Table III. *Meadow pipit.*

	Section				
	1	2	3	4	Total
Area of top and sides (acres)	244[2]	207	150	246	847
Number of pairs	75	105	45	50	275
Density (acres per pair)	3·1	2·0	3·3	4·9	3·1

Table IV. *Stonechat.*

	Section				
	1	2	3	4	Total
Area of top and sides (acres)	244[2]	207	150	246	847
Number of pairs	7	9	4	8	28
Density (acres per pair)	35	23	37½	31	30·2

In the case of the rock pipit and oyster-catcher, which nest all round the coast, the density is best described in terms of the distance separating pairs from one another.

Table V. *Rock pipit.*

	Section				
	1	2	3	4	Total
Approx. length of coast (yards)	4200	1800	1900	4500	12400
Number of pairs	19	5	5	12	41
Density (yards per pair)	220	300	380	375	300

[1] The area of the top only is given for the skylark, because it does not nest on the sides.

[2] 396 less 152 acres of farmed land, where these species are absent.

Table VI. *Oyster-catcher.*

	Section				Total
	1	2	3	4	
Approx. length of coast (yards)	4200	1800	1900	4500	12400
Number of pairs	3	4	3	4	14
Density (yards per pair)	1400	450	600	1100	900

The rock pipit is slightly more abundant on the east than on the west side in every section. In the case of the oyster-catcher, where the numbers are so small, the lengths of coast in each section are not sufficiently great to give an accurate idea of the uniformity of distribution.

CHANGES IN STATUS.

(a) *No change.*

In comparing past records with our own, the first fact to notice is that some species have remained fairly constant in numbers, especially the larger birds, e.g. the raven, peregrine, kestrel and buzzard. H. G. Hurrell and T. H. H. made a census of these species on the south coast of Devon in 1930, and found that, measured in pairs per mile, the density of the last two is very similar in both cases, though on Lundy the raven is relatively twice as abundant and the greater black-backed gull over twelve times as abundant. Buzzards apparently vary between two and four or even five pairs, probably due to fluctuations in the numbers of their main food supply, the rabbit. At seasons when the supply of rabbits is inadequate, an examination of pellets from Lundy by Dr Longstaff and C. Elton shows that dung beetles (Aphodiianae) form a main food item. The peregrine depends only to a very small extent on terrestrial birds for food in summer, being supported largely by kittiwakes at this time. Kestrels were found to feed largely on beetles, with an occasional pigmy shrew.

The numbers of oyster-catchers have remained unchanged. For the smaller birds figures are not generally available, but the chaffinch and stonechat at least are just about as numerous now as they were at the time of Loyd's visit eight years ago. Comparatively little change takes place in the vegetation of Lundy at the present time, and it is quite probable that the generally distributed species, for example the pipits and skylark, are not subject to much change either, except for fluctuations caused by "good" and "bad" years (see Harrisson (9) for further details).

A few species are represented by only one pair of breeding birds, or by solitary individuals. Of these the sedge warbler, yellow wagtail, common snipe and mallard are irregular breeders, scarcely able to find footing on the island owing to their preference for water or wet land, of which there is little to be had. Others, such as the blackcap and cuckoo, are present year after year. Mill Combe is the only place suitable for blackcaps; but in the case of the

cuckoo it is more difficult to understand what puts a check on the numbers when there are 275 pairs of meadow pipits available as foster-parents. We suggest that the reason may perhaps be the scarcity of trees and the absence of hedges for the cuckoos to perch in.

(b) Decreases.

A few species have declined to a marked extent, notably the yellow-hammer and corncrake. Of the former there were "six or eight pairs, confined to S.E. corner" in 1922 (Loyd). This year there were none, and apparently none have been noted since Loyd's visit. Though he found only one corncrake, several pairs have nested in recent years. In 1928 there were still two pairs: in 1929 only one pair stayed through the summer: and in 1930 there were none. The goldfinch and golden-crested wren, both represented by a single pair in 1922, were absent in 1930.

(c) Increases.

The increases on the other hand are in some cases astonishing. The greater black-backed gull has increased from twelve to about fifty, and the carrion crow from six to sixteen pairs. The lapwing has formed a small colony on Pondsbury (Section 2) since 1927 (as F. W. Gade and Dr Longstaff inform us). Four pairs of willow warblers bred this year, none having been previously recorded on reliable authority apart from passage birds. The song thrush has almost doubled its numbers since 1922. The most noteworthy increases, however, are those of the house-sparrow from five to twenty-two pairs, and of the hedge-sparrow from two in Section 2 (Loyd, 1922) to twenty-three this year along the whole extent of the east side.

An increase of warblers and thrushes is not surprising, because their main nesting place, Mill Combe, has grown up a good deal during the last eight years. However, there has been no increase in the number of houses to favour the house-sparrow; and the principal breeding area of the hedge-sparrow is the bracken zone, which has been in a climax condition for many years.

(d) Absentees.

It is difficult to explain the complete absence of jackdaws as breeding birds, confirmed by all recent observers, the more so because the jackdaw visits the island regularly (even daily) to feed. Other species which might be expected to breed, but which are not found, are the stock dove, starling, spotted flycatcher, chiffchaff and missel thrush. Starlings were known to roost on Lundy three centuries ago, and have also done so during the past few winters.

We are dealing with various systematic and other notes not relevant to the census in a separate paper to be published elsewhere (Harrisson (9)).

REFERENCES.

(1) **Alexander, C. J.** and **H. G.** *British Birds,* **2,** 322.

(2) **Burns, F. L.** *Wilson Bulletin,* p. 84, 1901.

(3) **Cooke, M. T.** *U.S. Dept. Agric., Dept. Bull.* 1165. (Washington, 1923.)

(4) **Forbes, S. A.** *Illinois State Lab. N.H. Bull.* **9,** 373; **14,** 187 and 397; etc.

(5) **Longstaff, T. G.** *Ibis,* p. 637, 1926.

(6) **Loyd, L. R. W.** *British Birds,* **16,** 148, 1922.

(7) **Moreau, R. E.** and **W.** This JOURN. **19,** 64, 1931.

(8) **Nicholson, E. M.** *Field,* Xmas Number, p. 34, 1926.

9) **Harrisson, T. H.** *British Birds,* **25,** 212, 1932.

THE VEGETATION OF ALBERTA

IV. THE POPLAR ASSOCIATION AND RELATED VEGETATION OF CENTRAL ALBERTA

By E. H. MOSS.

Botanical Laboratories, University of Alberta, Edmonton, Canada.

(With Plates XXII–XXV and three Figures in the Text.)

CONTENTS.

INTRODUCTION.

IN central Alberta there occurs a region, approximately 20,000 square miles (50,000 sq. km.) in area, which is dominated in large part by poplar. This region has come to be known as "Parkland" or the "Grove Belt," because during the period of settlement the area has presented a park-like appearance, groves of trees being generally intermixed with open areas, the latter either cleared spaces or grassland, often with a light growth of shrubs or small trees. From the vegetational point of view, however, these names as applied to a considerable part of this region are unfortunate, because less than one-half of the area can be properly regarded as Parkland or Grove Belt.

    The poplar area has been generally considered to be a transition belt between climatic formations, merging on the west with the Cordilleran Forest, on the north with the Northern Forest and on the south with the Prairie. A brief account of these climatic formations has been given in an earlier paper (6). The immediate object of the present investigation was to obtain

an adequate conception of the floristic composition of the poplar vegetation and to relate as fully as possible any variations in composition with climatic, edaphic and topographic factors. A further aim was to clarify our understanding of the relationships existing between the poplar vegetation and the adjoining climatic formations. It should be pointed out, however, that a clear understanding of the significance of the poplar belt and of relationships between the associated communities must await critical investigation of the Cordilleran Forest, Northern Forest and Prairie.

As indicated above, the poplar area has usually been looked upon as a broad transition belt between climatic formations, but it may be regarded in other ways, viz. (1) as itself a climatic, or possibly, an edaphic, formation; (2) as an extension of the Northern and Cordilleran Forests, probably, in the main, of the Northern Forest. At present, we are inclined to the latter view, but, as already stated, a definite conclusion must await further study. Regardless of the conclusion reached upon this question, the fact is that where poplar and coniferous associations merge an ecotone or tension zone is found, and likewise where poplar vegetation and prairie meet an ecotone occurs. The first of these ecotones is given brief consideration in the next paragraph and will be described more fully in connection with the account of the white spruce association. The second ecotone is the true Parkland or Grove Belt and will be described under that heading. Our present conception of the poplar and true Parkland areas is set forth in Fig. 1.

Certain coniferous species of the Northern and Cordilleran Forest extend into the poplar region. Of these the most important is *Picea albertiana* S. Brown, which not uncommonly becomes a prominent tree in river valleys, ravines and in certain other situations to be described in this paper. There is evidence that this species, rather than poplar, is to be regarded as the chief constituent of the climax vegetation for a considerable part of the region now dominated by poplar; and this leads one to the tentative conclusion that the poplar area belongs to the Northern Forest formation. The occurrence of *Picea mariana* (Mill.) B.S.P., *Larix laricina* (Du Roi) Koch, *Pinus Banksiana* Lamb. and *P. contorta* Dougl. in special habitats of the general poplar region has been described in earlier papers of this series. An observation that may be recorded here is the extension of *Abies balsamea* (L.) Mill. as far south as Flat Lake, about 100 miles (160 km.) north-east of Edmonton, where this species was found associated with *Picea albertiana*, *Betula papyrifera* and *Populus*.

During this investigation invaluable assistance in the solution of taxonomic problems has been freely given by the following specialists, and to these I wish to express my cordial thanks: Miss A. Lorrain Smith of the British Museum; Dr E. W. Erlanson, University of Michigan; Dr C. R. Ball, Washington, D.C.; Dr A. J. Grout, New Brighton, N.Y.; Mr A. LeRoy Andrews, Ithaca, N.Y.; Dr A. S. Hitchcock and Dr J. R. Swallen of the
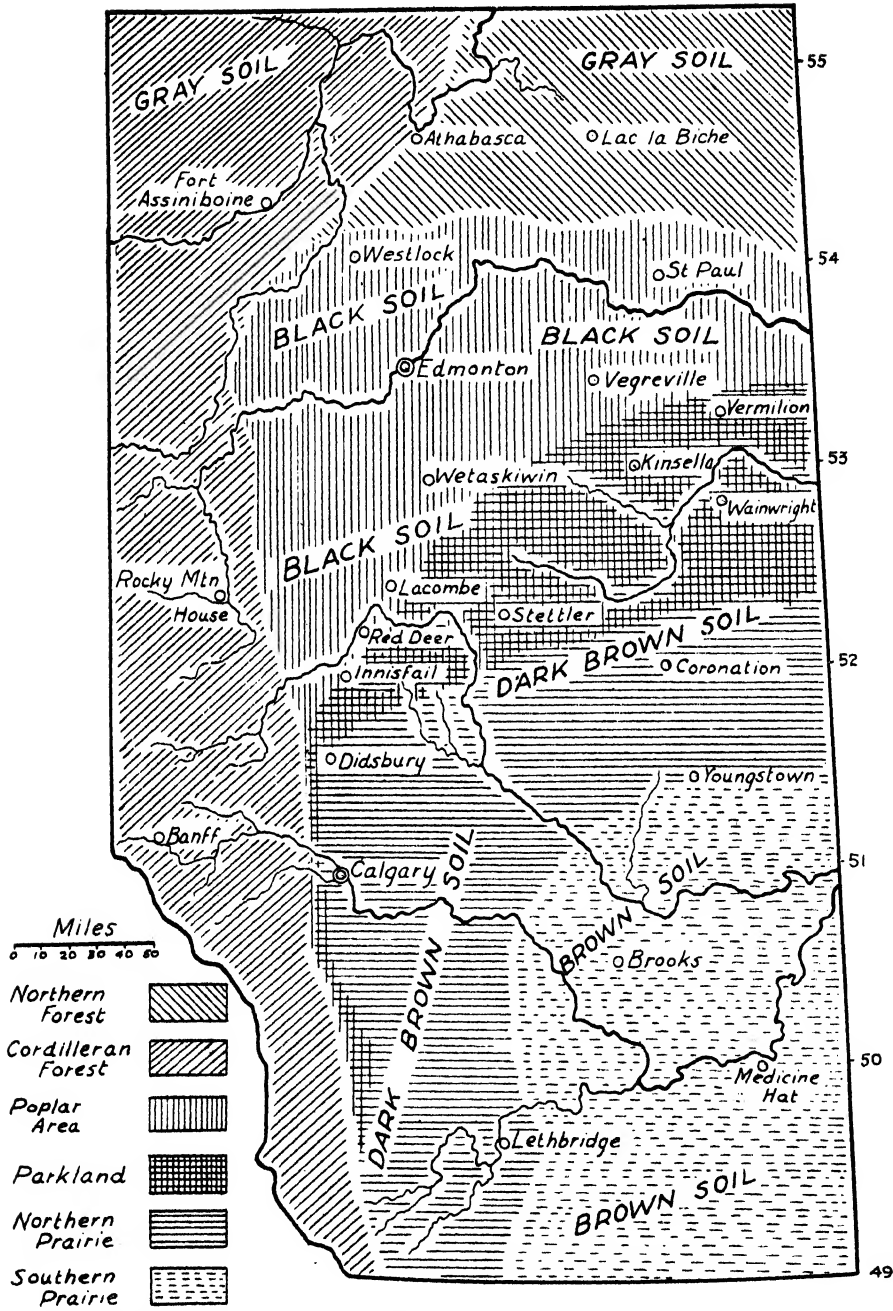
FIG. 1. Map of southern and central Alberta, showing the chief types of vegetation and soils.

Smithsonian Institution; Mr Kenneth K. Mackenzie, New York; Prof. L. O. Overholts, Pennsylvania State College; The Director of the Royal Botanic Gardens, Kew, and the Keeper of the Herbarium; Dr M. O. Malte of the National Herbarium, Ottawa. I am also indebted to Dr S. E. Clarke of the Dominion Range Experiment Station, Alta., and to Mr A. H. Brinkman, Craigmyle, Alta., for useful unpublished data on the local vegetation. To Prof. F. A. Wyatt of the University of Alberta, I am indebted for information concerning the soils of the area investigated. Finally, I wish to express my gratitude to Prof. F. J. Lewis for helpful suggestions during the investigation and the preparation of the manuscript.

TOPOGRAPHY, CLIMATE AND SOILS.

In an earlier paper (6) a brief description of the general topographical features of Alberta was given. At present we are concerned with part of the extensive undulating plateau which lies to the east of the Cordilleran region, and in particular with the areas occupied by poplar and parkland (Fig. 1). This plateau is traversed by several great river valleys which run east and north, while the general elevation gradually falls from 3000 ft. (900 m.) in the west and south to 2000 ft. (600 m.) in the east and north. In the vicinity of these river valleys the land is generally cut by numerous ravines and coulées. Much of the plateau is level to gently undulating in nature (Pl. XXV, phot. 9), while some parts are rolling to hilly. Extensive areas are characterised by hillocks with rounded contour, which have been largely formed by glacial deposits and post-Glacial erosion (Pl. XXV, phots. 7 and 8). In various parts of the region there are numerous, usually small, shallow lakes, locally known as sloughs.

Descriptions of the climate of Alberta have been given in an earlier paper of this series (6), and by Wyatt et al. (12). The climate of the region is typical of a continental climate of northern latitudes. It is characterised by long, cold, dry winters and by a growing season of about four months, May, June, July and August, during which the days are comparatively long, bright and moderately warm. It is further characterised by a rather light precipitation, of which at least 60 per cent. falls during the growing season and a considerable part of this during the month of June. This distribution of the precipitation is especially favourable to the development of grassland. Rainfall records taken over a period of 25 years show that the mean annual precipitation for the Southern Prairie of Alberta is about 13 in. and for the wooded areas about 17 in. In general the precipitation increases in amount from the south-eastern part of the province northward and westward to the Northern Forest and Cordilleran Forest respectively (Fig. 1). Owing to the prevailing low humidity, strong sunlight and frequent high winds, the rate of loss of water from the soil and from the vegetation is undoubtedly high. Meteorological records show that the evaporation from a free water surface is con-

siderably greater in the prairie than in the wooded areas (12), and indicate therefore that a unit of rainfall in the prairie region is less efficient in the development of vegetation than is a unit of rainfall in the forested areas. It may be stated, therefore, that the precipitation increases not only in amount but also in efficiency as one passes from the Southern Prairie north and west through the Northern Prairie, Parkland, and Poplar Area.

There is good reason to conclude that the climatic conditions briefly described above have been in large measure responsible for the development and persistence of the major plant communities of southern and central Alberta. There is also good reason to believe, according to students of soil science, that these types of vegetation have, in turn, been largely responsible for the production of the chief classes of soils found in the region. It should be added, however, that the climatic factors, and in particular precipitation, have had a marked direct effect upon the development of the soil types. Further, these various soils undoubtedly produce a considerable effect upon the vegetation which they support, tending either to maintain a climax state or to bring about vegetational succession. In view of these intimate and important interrelationships existing between climate, soils and plant communities, a consideration of the salient features of the more clearly defined soil types of our region will now be given. The following descriptions are taken from the publications of Wyatt and his collaborators (10, 11, 12).

The soils of the region have been developed, in the main, from glacial drift which covers most of the area to a depth of from a few inches to several hundred feet. This glacial material has been in part weathered from the underlying formations, in part brought in by glaciers. It is of two types, (1) glacial till or boulder clay, consisting of an unsorted mixture of clay, silt, sand, gravel and boulders, (2) resorted glacial deposits which have been deposited along old glacial drainage courses or in lakes near the retreating ice. The underlying formations are mainly of upper Cretaceous age and consist largely of sandstones and shales. In a few, comparatively small areas, devoid of drift covering, the soil is residual in origin, having been weathered *in situ* from the underlying rock. In other relatively small areas the soil has been derived from sand and clay deposits that have been transported and resorted in post-Glacial times, by running water or by wind.

The soils under consideration, like soils of dry climates in general, are characterised by the presence of a lime carbonate layer or horizon. This layer is formed at the depth to which the percolation water penetrates and where the carbonates and certain other salts crystallise out of solution and accumulate. These soils differ widely in structure, texture and chemical composition, but, in general, are very fertile. They are well provided with mineral plant foods and are especially rich in nitrogen and organic matter. The major soil classes recognised by Wyatt are based upon features of the soil profiles and are as follows:

(a) *Brown soil.* The profile of this soil is characterised by a relatively shallow horizon of brown loam, 8–14 in. (20–35 cm.) in thickness, and by the nearness of the lime layer to the surface, occurring at depths varying from 9 to 22 in. (23 to 56 cm.). The lime carbonate layer averages about 10 in. (25 cm.) in thickness and is greyish brown in colour, with the lime uniformly distributed. The surface horizon is neutral to slightly alkaline in reaction. This type of soil occupies an area which practically coincides with the Southern Prairie.

Soils intermediate in nature between *brown soil* and *black soil* occupy a broad belt between the Southern Prairie and the wooded regions, including the Northern Prairie and most of the Parkland; these may be referred to as *dark brown soils* (Fig. 1).

(b) *Black soil.* The profile is characterised by a deep surface layer of black soil, which is about 18 in. (46 cm.) in thickness and is particularly rich in organic matter and nitrogen, and by a lime horizon which is seldom found nearer the surface than 3 ft. (90 cm.). The lime layer averages about 6 in. (15 cm.) in thickness, is greyish in colour, with the lime in spots and streaks. The surface layer is neutral to slightly acid in reaction. This type of soil occurs mainly within the Poplar Area (Fig. 1). There is good reason to believe that the greater part of the black soil area was originally dominated by grasses and that the poplar vegetation has come in rather recently in soil history; this subject is considered more fully elsewhere in this paper.

(c) *Grey* or *wooded soil.* The profile is characterised by a distinct, thin, surface layer of organic matter, 1–4 in. (2·5–10 cm.) in thickness, by an underlying badly leached layer, greyish in colour and mainly ash-like, and by a horizon of lime accumulation at a depth of at least 4 ft. (120 cm.) below the surface. The surface horizons are distinctly acid in reaction, the pH values varying from 6·0 to 6·8. This soil is closely related to the podsols of northern Europe, but, according to Wyatt, differs from podsol in being a younger soil and not so well developed. This is the principal type of soil in the Northern and Cordilleran Forests. It occurs also in certain parts of the Poplar Area, particularly in morainic sections and towards the north and west.

Chemical analysis has shown that these various soils are well provided with plant foods, but that the grey soils are in general much less fertile than the black and brown soils. Wyatt and Ward (**11**) state their findings as follows: "The mineral plant foods are less abundant in the wooded soils than in the black and brown soils. The first foot of the black soil contains six times as much nitrogen, twice as much calcium and more magnesium than is found in the same depth of the wooded soil."

Within the general area occupied by grey soils and also in the transition zone between black and grey soil belts are to be found soils intermediate in character between typical black and typical grey soils. Many of these transition soils undoubtedly were at one time typical black soils that had been

formed under prairie conditions; but, after having supported a forest vege-
tation for many years, probably for centuries, they have become more or less
markedly leached, commonly exhibiting at the present time a prominent
greyish stratum in the rather broad black horizon. Granted that black or
prairie soils are being thus transformed into the grey or wooded type, we have
here a useful means of studying the ecotone between prairie and forest
vegetation.

<center>THE POPLAR ASSOCIATION.</center>

<center>(a) *General description.*</center>

Although a large part of the Poplar Area (Fig. 1) has been brought under
cultivation or otherwise disturbed, one can still locate numerous poplar stands
that are undoubtedly in the virgin state. About a hundred such stands,
situated in representative parts of the area, were given critical study. In-
cluded were stands of various ages and stands growing under widely different
edaphic and physiographic conditions.

There are in central Alberta two species of *Populus*, namely, *P. tremuloides*,
the aspen, and *P. balsamifera*, the balsam poplar. The aspen extends through-
out the entire region under consideration, and occurs over a wide range of
edaphic conditions, including dry knolls, moist river flats and such soils as
loam, clay and sandy. The balsam poplar is much more restricted in its distri-
bution, being comparatively uncommon in the Parkland and southern part
of the Poplar Area but becoming quite frequent northward and westward.
It reaches its best development in the more moist situations, such as river
flats, being of rare occurrence in dry, exposed sites. Apparently it is con-
siderably more exacting in its water requirements than is the aspen. There is
good evidence that the aspen is the climax tree of the drier and generally
more southern parts of our region, while the balsam poplar is the sub-climax
tree (*Picea albertiana* being the climax species) of the more moist situations,
especially in the northern and western parts of the region.

Since these two dominant species occur typically in different habitats and
since, as will be shown later, each is accompanied by certain characteristic
species, we are led to recognise two types of poplar vegetation, namely, Aspen
and Balsam Poplar consociations. Further consideration is given to this
subject on p. 397.

<center>(b) *Tree data, site quality and climatic cycles.*</center>

The aspen and the balsam poplar are generally reproduced by suckers from
roots near the surface of the soil. By means of these suckers the species may
gradually spread into an adjoining community such as the prairie. Following
burning of a poplar stand, a dense growth of shoots springs from the under-
ground parts of the burned trees; and so the poplar community perpetuates
itself and may continue to occupy an area in spite of fairly frequent burnings.

A stand initiated in this way commonly contains, at the age of 5 years, about 500 trees per hundred square metres, but of these, less than 10 per cent. reach an age of 30 years and only a very small percentage attain to old age (Table I). The high mortality of trees in younger stands is undoubtedly due to crowding, the smaller and weaker trees being killed in the keen competition for light, water and nutrients. In older stands tree growth slows down, and therefore thinning due to crowding progresses more slowly; but here a new factor enters, namely, the elimination of trees due to depredations of wood-rotting fungi, particularly *Fomes igniarius* (L.) Gillett. This heart-rotting polypore is very destructive to the aspen, especially to trees exceeding 50 years of age. Studies on a few 70-year stands showed that about 15 per cent. of the standing trees were dead, due largely to injury by fungi, while, of the living trees, about 15 per cent. bore sporophores of *Fomes*. Infection by this fungus occurs in aspens much younger than 70 years, sporophores of *Fomes* being not uncommon on trees of 50 years, rarely on trees of about 35 years. The balsam poplar appears to be less susceptible than the aspen to attack by wood-destroying organisms; nevertheless, older trees are usually more or less decayed in the heartwood, presumably due to fungous activity. Whether *Fomes igniarius* is the parasite in this case is not apparent, because no sporophores of this fungus have been observed by the writer on the balsam poplar. Nor indeed have sporophores of any other wood-destroying fungi been found on living balsam poplars. Fungi found associated with dead poplars include *Fomes applanatus* Pers., *Armillaria mellea* Vahl., and *Pleurotus* spp., of which *P. ostreatus* Jacq. is rather common on the aspen.

Table I. *Rate of thinning of poplar stands as shown by the approximate number of trees in stands of different ages.*

Age in years	No. of trees per 100 sq. m.
5	500
10	250
15	175
20	80
30	45
35	40
50	25
70	10
110	3

The rate of growth in height of poplars has been critically studied in Minnesota by Kittredge and Gevorkiantz (5), and shown to be closely correlated with the productivity of the soil, or *quality of site*. Utilising data giving heights and ages of dominant trees in aspen stands, these investigators have derived *site index curves*, which are claimed to be quite useful in making determinations of site quality. In Fig. 2 are shown site index curves which are believed to be applicable to poplar stands in Alberta. These curves are, in most respects, modelled after those published by Kittredge and Gevorkiantz, but have been carefully checked by means of a considerable amount of data

obtained from poplar stands in our area. The *site index* is defined as the average height of the dominant trees in a stand at 50 years; or, in the case of a younger stand, the height that would be reached by the dominant trees at 50 years. In general, we find that stands with low site indices occur in dry, exposed situations such as south-facing slopes, or on inferior soils, for example, sandy and morainic soils. On the other hand, stands with high site
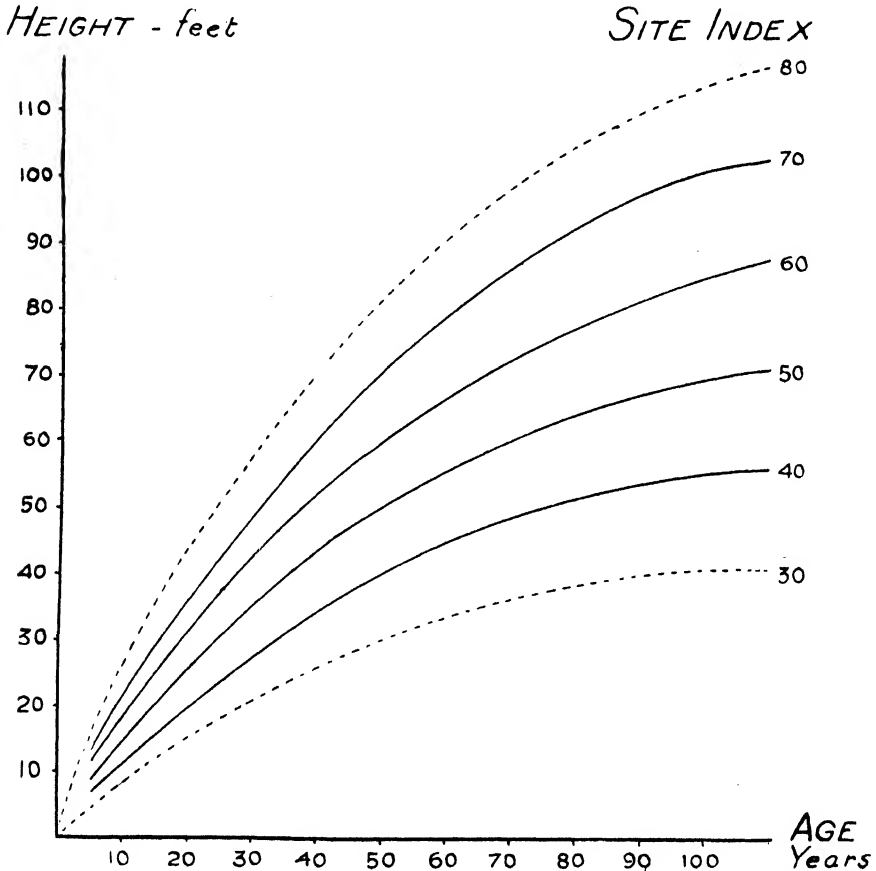

FIG. 2. Site index curves for poplar in Alberta.

indices usually occur in situations where the soil moisture is well conserved and on deep black and other superior soils. In our area, the range in site index is from about 30 to about 80, and for most of the stands studied is between 50 and 60. There appears to be no appreciable difference, as a rule, between the site indices of aspen and balsam poplar when growing under the same conditions, for example, when intermixed, or when occurring as pure stands in adjoining areas whose soil and topographical features are essentially alike. There is some indication, however, that on the better sites, balsam

Phot. 2. Balsam Poplar-Spruce stand; poplars 135 years old and about 110 feet high; ground cover mainly *Hypnum-Hylocomium* mosses and *Equisetum*.

Phot. 1. Aspen stand, 70 years old, with trees over 90 feet high; white spruce in background.

MOSS—THE VEGETATION OF ALBERTA. IV. THE POPLAR ASSOCIATION AND RELATED VEGETATION OF CENTRAL ALBERTA

poplar grows more rapidly than the aspen; and in such cases, therefore, the balsam poplar would have a higher site index than the aspen.

Of considerable interest is the relationship between site indices and the occurrence of the two poplar species. The balsam poplar has been found dominant on no area with a site index below 50 and rarely where the site index is below 55. The aspen, on the other hand, appears to be less exacting in its requirements, for it occurs as a dominant on both the better and poorer sites. On the latter, aspen stands are usually well developed even though the trees make comparatively slow growth. On the better sites, the aspen grows exceedingly well, both in pure stands and where intermixed with balsam poplar, commonly attaining on the best sites a height of 90 ft. (27 m.) in 70 years (Pl. XXII, phot. 1). Nevertheless, superior sites are usually dominated by the balsam poplar. Furthermore, there is some evidence that superior sites now dominated by aspen may eventually become dominated by balsam poplar, as a consequence of the latter species having a longer span of life than the aspen, and possibly also because the balsam poplar grows more rapidly on the better sites, thus tending to crowd out the aspen by shading. Of significance in this connection is the fact that aspen stands occurring on superior sites have a shrub and herb vegetation which is characteristic of balsam poplar stands. The conclusion may therefore be drawn that the two poplar species characterise markedly different sites or habitats; and, as will be pointed out later (p. 397), this conclusion has had an important bearing on the recognition of two consociations in the poplar vegetation of our area.

Only brief reference will be made here to growth in girth of poplar trees. In every even-aged stand, there are found wide differences in the diameters of the trees, even of the dominant individuals (that is, those whose tops form the general canopy of the stand). Some conception of the rate of growth in diameter may be had from the following data. Approximate figures for average D.B.H. (diameter at breast height) of dominant trees in fairly good aspen stands of 35, 70 and 110 years are respectively 15, 24 and 30 cm.; and in superior aspen stands of 70 and 110 years are respectively 35 and 50 cm. In general, the balsam poplar has a more rapid growth in diameter than the aspen, a difference which becomes quite pronounced among older trees, because the balsam poplar has a longer span of life than the aspen. On the best sites; the balsam poplar attains an average D.B.H. at 70 years of about 45 cm. and at 135 years about 75 cm. (Pl. XXII, phot. 2). The largest balsam poplar observed was approximately 135 years old and measured 110 cm. in diameter and about 118 ft. (36 m.) in height.

As a rule, the trees of a particular poplar stand are of the same age, or very nearly so. The explanation of this uniformity in age is that the trees of the stand started as suckers shortly after a complete burning off of the parent stand. By finding the age of a stand one can determine the date, within about a year, at which the parent stand was burned. Age determinations were made

of a large number of stands generally distributed in our area, a Swedish increment borer being used to obtain cores for counts of annual rings; and the results are set forth in Table II. The significance of the facts concerning the prevailing ages of stands, namely, 9 to 20, 30 to 38, 50, 70 and 110 years, and the conclusions in regard to the dates of general burning in our area will now be discussed.

According to our records the balsam poplar rarely exceeds 135 years, the aspen 120 years, in age. Most of the older trees were so badly decayed in the heart that their exact age was indeterminable. These older trees only occasionally comprise the bulk of a stand, for most of the sister trees have died, due to old age and fungus attack or to burning. Such partial burning of a stand may have occurred on one or more occasions in the past, with the result that the older trees commonly have associated with them younger trees of one or more generations. A point of especial interest is that the ages of these younger generations almost invariably correspond with the prevailing ages of uniform stands, that is 30–38, 50 and 70 years; this provides additional evidence that general burning occurred at the dates shown in Table II. It may be added that, in stands containing trees of two or more generations, a number of the older trees usually showed distinct signs of fire injury in the basal parts of their trunks. Also in a number of cases, borings of older trees showed burn scars at the ages corresponding to certain of the dates of general burning.

The occurrence of a large number of stands ranging in age from 20 down to 9 years indicates that fires were quite prevalent between the years 1908 and 1919. The first part (1908–12) of the period was marked by a great influx of settlers and general clearing of the poplar region, much of which, however, was not broken but was for various reasons abandoned, consequently giving rise to new stands of trees. The last part (1918–19) of the period had a markedly low rainfall, a fact which may in part account for so much burning at that time. During the decade since 1919 conditions have been more stabilised, fires have usually been kept within bounds, and the numerous wooded areas cleared by cutting and burning have usually been immediately broken and used for agricultural purposes.

The general burning that occurred between 1890 and 1898 may be correlated with two historical facts. In the first place, early settlers report that exceptionally arid conditions prevailed, that the shallower lakes dried up and the level of the larger lakes was unusually low; evidently, therefore, this was a period of very low rainfall, and a time when extensive burning would be likely to occur. Secondly, during this period the first railroad reached our area, bringing a considerable number of settlers; and these settlers undoubtedly initiated many fires, some of which may have swept over extensive areas. Since very little burning seems to have occurred between 1898 and 1908, we conclude that this period, at least the early part of it, was characterised by a

high precipitation. Rainfall records for Edmonton show that there was an exceptionally heavy precipitation in 1899, 1900 and 1901.

The dates 1878, 1858 and 1818 given in Table II are regarded only as close approximations to times of general burning. Also, the evidence obtained for the dates 1878 and 1858 is much more convincing than that obtained for 1818. Furthermore, since 70-year stands are considerably more numerous than 50-year stands, one is inclined to believe that burning was more general in 1858 than in 1878. During those earlier times, fires were started presumably by lightning, by Indians or by explorers; and such fires would probably become widespread and burn off the region as a whole only after dry climatic conditions had prevailed generally for a period of time. On the assumption that extensive burning is correlated with prolonged drought conditions, the conclusion may be drawn that these dates of general burning brought to a close periods during which extremely arid conditions prevailed. It may be further concluded that an unusually heavy precipitation occurred during the year or years immediately following these dates; otherwise, the extremely dry conditions that favoured general burning would not have been so effectively offset. Indeed, it is quite probable that heavy precipitation may have occurred even earlier than these various dates, but, because of the prevailing aridity, was ineffectual in preventing general burning.

Table II. *Occurrence of poplar stands of different ages, and dates of burning of parent stands.* (*Studies made in* 1929.)

Ages in years	Frequency of occurrence		Dates —burning of parent stands	Hypothetical climatic cycles
1– 8	Several	observed	1928 ←- 1920	—
9–10	Very many	,,	1919 ←- 1918*	—
12–15	Many	,,	1916 ←- 1913*	
16–20	Very many	,,	1912 ← 1908*	
21–29	Very few	,,	1907 ← 1899	20 years
30–38	Very many	,,	1898 ← 1890*	
39–49	None	,,	1889 ← 1879	
50	Several	,,	1878*	20 years
51–69	Very few	,,	1877 ← 1859	
70	Very many	,,	1858*	20 years
71–95	Very few	,,	1857 ← 1833	
100†	Small number	,,	?	40 years
110 (accurate)	Small number	,,	1818*	(20 + 20)
115–135†	Small number	,,	?	—

* Regarded as dates of general burning.
† Exact ages could not be determined because of decayed condition of the heart wood.

For the purpose of setting forth a hypothesis concerning climatic cycles, as indicated in Table II, we shall now assume that the foregoing discussion has established the following: (1) that the dates of general burning shown in the table are approximately correct; (2) that these dates terminated periods of general drought in the poplar region, and that the periods immediately following (if not, indeed, immediately preceding) these dates were exceptionally wet. The hypothesis is that climatic cycles, about 20 years in length,

have occurred in our region, and that each of these cycles has been characterised by a period of extremely dry climatic conditions, followed by a period of heavy precipitation. As already indicated, the wet phases of these climatic cycles appear to have commenced not later (and probably earlier) than 1819, 1859, 1879 and 1899. Extensive burning during the period 1908–19 is thought to have been due not so much to dry climatic conditions as to human activities. Rainfall records and other reports indicate that rather dry conditions prevailed in 1908–10, and that this was followed by a markedly wet period, 1912–16. The latter period should have come about 5 years later in order to assume its proper place in a rigid scheme of 20-year cycles as indicated above. The period 1917–30 has been, in the main, one of low rainfall and drying winds, with the result that the levels of lakes have become unusually low, a situation not unlike that of the early "nineties." There is every indication, therefore, that we are now passing through a dry phase of a 20-year climatic cycle; and if so, a wet phase may be expected to begin between 1932 and 1939, probably about 1935.

This hypothesis will we hope be critically tested in the near future by means of additional data of the kind already collected, and also by studies of the annual rings of a large number of trees, spruce and pine as well as poplar, from various parts of the region, with a view to determining to what extent rate of growth can be correlated with the critical phases in the hypothetical climatic cycles.

(c) *Floristic composition and ecological structure.*

The floristic composition of the poplar vegetation is set forth in Table III. This list is not to be regarded as nearly complete, for further examination of the poplar vegetation will certainly reveal many additional species. Of some 217 species recorded, 178 are vascular plants and 39 are mosses and lichens. The 178 vascular plants comprise 8 Pteridophytes, one Conifer and 169 Angiosperms. At least 200 of these species are considered to be natural and typical constituents of the poplar community. A very few, for example, *Taraxacum officinale* and *Phleum pratense*, are introduced species. A small number belong more properly to other communities of the region, for example, *Festuca scabrella* to the Northern Prairie association; *Vaccinium* spp. to muskeg and pine associations.

Numerous taxonomic and nomenclatural problems have been encountered. Some of the more important of these may be noted here, while others are indicated in the accompanying table. The willow reported as *Salix mackenziana macrogemma* Ball in a former paper (6) is now tentatively referred to the species *myrtillifolia* by Dr C. R. Ball. The various species and varieties of *Rosa* were rarely distinguished in the field, and consequently are grouped together in the table. Numerous collections of *Rosa* were made and a considerable number of these were kindly examined by Dr E. W. Erlanson, who

reports the various forms listed. Field observations made in the light of Erlanson's reports and descriptions (3) indicate that *R. acicularis* var. *Sayiana* is the most common of the roses in the poplar vegetation. Included under the name *Aster Lindleyanus* is a diversity of forms, some of which may perhaps be referable to other species; this complex would merit critical study. Forms intermediate between typical *Agropyron tenerum* and typical *A. Richardsoni* were commonly encountered. Peto (8) who has recently studied these and other species of *Agropyron* in Alberta presents morphological and cytological evidence in support of the conclusion that natural hybridisation occurs between certain of these grasses and he suggests that this may account for the wide range of variability found both within and between the so-called species of this genus.

Table III. *Composition of the poplar association.*

Species	Constancy: percentage of stands in which species were found			Frequency indices of species		
	Balsam stands	Balsam-aspen stands	Aspen stands	Balsam-poplar conso-ciation	Balsam-aspen vege-tation	Aspen conso-ciation
A. *Taller trees.*						
Betula papyrifera Marsh.	46	33	37	0·9	0·8	0·6
Populus balsamifera L.	100	100	73	86·0	52·0	3·0
P. tremuloides Michx.	87	100	100	5·7	44·0	96·0
Picea albertiana S. Brown	53	25	12	4·7	0·5	0·1
B. *Smaller trees and larger shrubs.*						
Alnus incana (L.) Moench.	53	8	3	5·1	2·8	0·1
Alnus sp.	7	0	0	0·1	—	—
Amelanchier alnifolia Nutt.	34	75	94	1·8	5·6	8·6
Cornus stolonifera Michx.	95	75	64	18·4	8·6	4·1
Prunus melanocarpa (A. Nels.) Rydb.	46	42	80	1·6	4·2	5·4
P. pennsylvanica L.	0	17	50	—	0·4	2·1
Salix arbusculoides And.	7	0	0	0·3	—	—
S. balsamifera (Hook.) Barratt	20	0	0	0·4	—	—
S. bebbiana Sarg. / S. bebbiana perrostrata (Rydb.) Schn.	90	75	57	4·4	6·0	2·6
S. discolor Muhl.	60	50	34	1·1	0·8	0·5
S. lutea Nutt.	7	0	0	0·1	—	—
S. maccalliana Rowley	14	8	0	0·1	0·1	—
S. myrtillifolia Anders.	67	25	7	4·7	1·8	0·1
S. petiolaris J. E. Smith	7	0	0	0·1	—	—
S. planifolia Pursh.	20	0	0	0·6	—	—
S. pseudomonticola Ball	7	8	3	0·1	0·1	0·1
Viburnum Opulus L.	14	25	14	1·1	0·6	0·9
C. *Smaller shrubs.*						
Betula glandulosa Michx.	14	8	0	0·1	0·1	—
Clematis verticillaris DC.	7	0	0	0·1	—	—
Corylus rostrata Ait.	27	42	60	0·8	5·1	9·4
Elaeagnus argentea Pursh.	0	0	7	—	—	0·2
Ledum groenlandicum Oeder.	21	0	0	0·4	—	—
Lonicera glaucescens Rydb.	60	75	60	1·5	1·0	0·6
L. involucrata (Richards.) Banks	90	67	30	4·2	1·8	0·6
Rhamnus alnifolia L'Hér.	7	0	0	0·3	—	—
Ribes americanum Mill.	54	8	0	1·6	0·1	—
R. glandulosum Grauer	40	8	0	2·0	0·1	—
R. hudsonianum Richards.	54	11	10	2·6	0·2	0·1
R. lacustre (Pers.) Poir	26	8	0	0·8	0·1	—

Table III (*cont.*).

Species	Constancy: percentage of stands in which species were found			Frequency indices of species		
	Balsam stands	Balsam-aspen stands	Aspen stands	Balsam-poplar conso-ciation	Balsam-aspen vege-tation	Aspen conso-ciation
R. oxyacanthoides L. } R. setosum Lindl.	84	75	70	3·1	1·4	1·0
R. triste Pall.	35	50	20	0·8	1·1	0·4
Rosa acicularis Lindl. var. Sayiana Erlanson „ Bourgeauiana Crépin „ lacorum Erlanson „ rotunda Erlanson R. Fendleri Crépin R. Macounii Greene	100	100	97	14·4	22·4	18·2
Rubus strigosus Michx.	90	91	87	7·8	5·9	5·5
Shepherdia canadensis (L.) Nutt.	26	17	17	0·7	0·1	0·1
Spiraea alba Du Roi	7	0	7	0·1	—	0·1
Symphoricarpos occidentalis Hook.	18	17	24	0·2	0·5	1·9
S. pauciflorus (Robbins) Britton	66	91	80	3·6	8·9	11·9
Viburnum pauciflorum Pylaie	90	100	77	8·5	10·1	10·8
Vaccinium canadense Kalm.	7	0	3	0·1	—	0·1
V. caespitosum Michx.	7	0	3	0·1	—	0·1
V. Vitis-Idaea L.	14	0	0	0·3	—	—

D. *Taller herbs.*

Species	Balsam stands	Balsam-aspen stands	Aspen stands	Balsam-poplar conso-ciation	Balsam-aspen vege-tation	Aspen conso-ciation
Achillea lanulosa Nutt. } A. millefolium L.	28	34	34	0·4	0·6	0·6
A. multiflora Hook.	0	0	17	—	—	0·1
Actaea eburnea Rydb.	56	25	17	0·5	0·2	0·1
A. rubra (Ait.) Willd.	84	67	40	0·7	0·6	0·3
Agastache anethiodora (Nutt.) Britton	7	34	40	0·1	0·2	0·2
Agrimonia striata Michx.	14	19	7	0·1	0·1	0·1
Agropyron Richardsoni Schrad.	84	75	77	5·2	5·7	5·5
A. tenerum Vasey	90	100	80	7·8	5·9	5·9
Agrostis hyemalis (Walt.) B.S.P.	0	0	3	—	—	0·1
Allium cernuum Roth.	7	17	7	0·3	0·4	0·1
Anemone canadensis L.	35	34	20	0·5	0·4	0·2
A. virginiana L.	14	17	20	0·1	0·1	0·2
Antennaria pulcherrima (Hook.) Greene.	7	0	0	0·1	—	—
Apocynum scopulorum Greene	14	0	24	0·1	—	0·2
Aquilegia brevistyla Hook.	0	8	0	—	0·1	—
Aralia nudicaulis L.	77	67	87	6·9	7·7	13·0
Aspidium spinulosum (O. F. Müller) Sw.	21	0	0	0·2	—	—
Aster conspicuus Lindl.	35	17	44	0·5	0·9	1·0
A. laevis L.	0	0	27	—	—	0·4
A. Lindleyanus T. and G.	95	100	97	11·3	18·1	14·4
A. modestus Lindl.	7	8	3	0·1	0·1	0·1
A. puniceus L.	7	8	0	0·1	0·1	—
A. umbellatus Mill. var. pubens Gray	14	8	0	0·3	0·1	—
Botrychium virginianum (L.) Sw.	14	8	3	0·2	0·1	0·1
Bromus ciliatus L.	56	58	74	3·5	3·8	4·3
B. Pumpellianus Scribn.	7	0	7	0·1	—	0·1
Calamagrostis canadensis (Michx.) Beauv.	90	91	87	12·8	9·2	8·7
Campanula rotundifolia L.	7	0	14	0·1	—	0·1
Castilleja ? rhexifolia Rydb.	21	8	0	0·1	0·1	—
Chenopodium hybridum L.	7	0	0	0·1	—	—
Cinna latifolia (Trev.) Griseb.	14	0	0	0·3	—	—
Cirsium sp.	7	0	0	0·1	—	—
Corallorrhiza Corallorrhiza (L.) Karst.	7	0	3	0·1	—	0·1
C. striata Lindl.	7	8	0	0·1	0·1	—
Cypripedium parviflorum Salisb.	7	17	0	0·1	0·2	—
Cystopteris fragilis (L.) Bernh.	7	0	0	0·1	—	—
Delphinium Brownii Rydb.	7	8	3	0·1	0·1	0·1

Table III (cont.).

Species	Constancy: percentage of stands in which species were found			Frequency indices of species		
	Balsam stands	Balsam-aspen stands	Aspen stands	Balsam-poplar conso-ciation	Balsam-aspen vege-tation	Aspen conso-ciation
Disporum trachycarpum S. Wats.	28	50	64	0·5	0·7	0·6
Elymus innovatus Beal	7	42	37	0·1	1·0	2·4
Epilobium angustifolium L.	95	91	77	6·3	10·6	6·6
Erigeron philadelphicus L.	28	0	0	0·1	——	——
Erysimum sp.	0	0	3	——	——	0·1
Galium boreale L.	84	100	90	4·6	9·2	9·9
G. triflorum Michx.	84	75	20	4·8	1·7	0·3
Gentiana plebeia Cham.	28	8	17	0·1	0·1	0·1
Geranium strigosum Rydb.	28	42	20	0·8	1·1	0·2
Geum macrophyllum Willd.	0	17	0	——	0·1	——
G. strictum Soland.	14	25	7	0·1	0·2	0·1
Glyceria nervata (Willd.) Trin.	7	8	0	0·1	0·1	——
Habenaria bracteata (Willd.) R.Br.	7	17	17	0·1	0·1	0·1
Halenia deflexa (Smith) Griseb.	7	0	0	0·1	——	——
Hedysarum boreale Nutt.	0	17	3	——	0·1	0·1
Heracleum lanatum Michx.	42	75	50	0·7	1·0	0·3
Impatiens biflora Walt.	7	0	0	0·1	——	——
I. occidentalis Rydb.						
Lactuca pulchella (Pursh.) DC.	0	0	3	——	——	0·1
Lappula sp.	0	0	3	——	——	0·1
Lathyrus ochroleucus Hook.	84	91	94	1·0	6·2	5·9
L. venosus Muhl.	0	25	24	——	0·6	1·5
Lilium umbellatum Pursh.	14	0	0	0·1	——	——
Mertensia pilosa (Cham.) DC.	90	67	74	12·1	10·0	6·1
Monarda menthaefolia Benth.	0	8	17	——	0·1	0·1
Muhlenbergia sp.	0	0	3	——	——	0·1
Oryzopsis asperifolia Michx.	0	0	7	——	——	0·1
Osmorhiza obtusa (Coult. and Rose) Fernald	0	0	3	——	——	0·1
Parnassia palustris L.	21	0	0	0·1	——	——
Petasites sagittata (Pursh.) A. Gray	21	0	0	0·1	——	——
Phaca americana (Hook.) Rydb.	28	17	3	0·4	0·5	0·1
Phegopteris Dryopteris (L.) Fée.	7	0	0	0·1	——	——
Phleum pratense L.	7	0	7	0·1	——	0·1
Poa palustris L.	42	17	14	0·6	0·4	0·3
P. pratensis L.	14	0	10	0·1	——	0·1
Potentilla sp.	14	0	7	0·1	——	0·1
Rhus Toxicodendron L.	0	0	3	——	——	0·1
Sanicula marilandica L.	14	42	47	0·1	0·7	0·6
Schizachne purpurascens (Torr.) Swallen	42	50	57	0·9	3·4	4·3
Senecio sp.	14	0	0	0·1	——	——
Sisymbrium canescens Nutt.	0	0	3	——	——	0·1
Smilacina stellata (L.) Desf.	84	91	57	1·0	1·2	1·3
Solidago canadensis L.	63	75	34	1·7	0·9	0·4
S. serotina Ait.	35	34	40	0·3	0·3	0·5
S. elongata Nutt.	0	0	3	——	——	0·1
Stachys scopulorum Greene	7	8	3	0·1	0·1	0·1
Steironema ciliatum (L.) Raf.	21	25	30	0·4	0·3	0·2
Thalictrum venulosum Trelease	70	91	60	1·7	9·6	4·7
Thalictrum sp.	7	0	0	0·1	——	——
Urtica gracilis Ait.	7	0	0	0·1	——	——
Valeriana septentrionalis Rydb.	7	0	0	0·1	——	——
Vicia americana Muhl.	84	91	97	1·9	3·2	2·6
Zizia cordata (Walt.) Koch.	0	0	3	——	——	0·1

E. *Lower herbs.*

Arenaria laterifolia L.	21	50	17	0·1	0·5	0·4
Carex concinna R.Br.	0	0	3	——	——	0·1
C. Deweyana Schwein.	14	0	0	0·3	——	——

Table III (*cont.*).

Species	Constancy: percentage of stands in which species were found			Frequency indices of species		
	Balsam stands	Balsam-aspen stands	Aspen stands	Balsam-poplar consociation	Balsam-aspen vegetation	Aspen consociation
C. capillaris L.	21	0	3	0·6	—	0·1
C. festivella Mackenzie	7	0	0	0·1	—	—
C. practicola Rydb.	0	0	3	—	—	0·1
C. saltuensis Bailey	7	0	0	0·3	—	—
C. siccata Dewey	0	0	7	—	—	0·3
Chrysosplenium sp.	7	0	0	0·1	—	—
Circaea alpina L.	21	8	0	0·2	0·1	—
Comandra livida Richards.	7	0	0	0·1	—	—
Cornus canadensis L.	70	83	77	2·8	4·3	11·9
Equisetum arvense L.	100	83	44	10·4	5·6	2·2
E. pratense Ehrh.	28	0	0	1·6	—	—
E. scirpoides Michx.	14	8	0	0·7	0·4	—
E. sylvaticum L.	14	0	10	0·4	—	0·1
Festuca scabrella Torr.	0	0	3	—	—	0·1
Fragaria americana (Porter) Britton } F. virginiana Duchesne }	90	100	90	7·5	14·2	10·1
Habenaria obtusata (Pursh.) Richards.	0	0	3	—	—	0·1
Linnaea borealis L. var. americana (Forbes) Rehder	70	58	47	10·0	5·5	5·8
Malaxis monophylla (L.) Sw.	0	8	0	—	0·1	—
Maianthemum canadense Desf.	63	83	87	2·5	8·0	9·3
Mitella nuda L.	70	50	17	4·7	1·7	0·3
Moneses uniflora (L.) A. Gray	7	0	0	0·1	—	—
Orchis rotundifolia Pursh.	14	0	0	0·4	—	—
Petasites palmata (Ait.) A. Gray	84	75	44	7·2	4·7	1·3
P. vitifolia Greene	14	14	0	1·7	0·4	—
Pyrola asarifolia Michx.	63	75	80	3·7	4·7	6·1
P. chlorantha Swartz	14	0	0	0·2	—	—
P. elliptica Nutt.	20	25	37	0·7	0·6	1·2
P. secunda L.	21	17	40	0·7	0·5	1·0
Rubus arcticus L.	7	0	0	0·1	—	—
R. triflorus Richards.	95	100	97	17·3	16·6	12·8
Stellaria longifolia Muhl.	0	0	3	—	—	0·1
S. longipes Goldie	7	0	0	0·1	—	—
Taraxacum officinale Weber	42	42	20	0·2	0·2	0·1
Trientalis americana Pursh.	0	0	3	—	—	0·1
Viola canadensis L.	70	91	90	6·1	16·2	9·9
V. renifolia Gray	28	0	20	1·0	—	0·1

F. *Mosses and lichens.*

Species	Balsam stands	Balsam-aspen stands	Aspen stands	Balsam-poplar consociation	Balsam-aspen vegetation	Aspen consociation
Aulacomnium palustre (L.) Schwaegr.	28	16	3	2·5	1·5	0·2
Brachythecium oxycladon (Brid.) Jaeg. and Sauerb.	0	8	3	—	1·0	0·2
B. albicans occidentale	0	0	3	—	—	0·1
B. salebrosum (Hoffm.) Br. and Sch.	7	0	0	0·1	—	—
Brynum caespiticum L.	7	16	3	1·0	1·6	0·1
B. turbinatum (Hedw.) Schwaegr.	0	0	10	—	—	0·1
Camptothecium nitens (Schreb.) Schimp.	7	8	0	1·0	1·0	—
Campylium hispidulum	0	0	3	—	—	0·1
Ceratodon purpureus (L.) Brid.	14	8	10	0·1	0·1	1·0
Climacium dendroides (L.) Web. and Mohr.	7	8	3	0·5	1·0	0·2
Dicranum Bergeri Bland	14	0	0	0·2	—	—
D. Bonjeani De Not.	7	0	0	0·1	—	—
D. elongatum	7	0	0	0·1	—	—
Eurhynchium strigosum (Hoffm.) Br. and Sch.	14	16	0	0·2	0·5	—
Hylocomium splendens (Hedw.) Br. and Sch.	35	25	7	3·0	1·3	0·1

Table III (*cont.*).

Species	Constancy: percentage of stands in which species were found			Frequency indices of species		
	Balsam stands	Balsam-aspen stands	Aspen stands	Balsam-poplar conso-ciation	Balsam-aspen vege-tation	Aspen conso-ciation
Hypnum Schreberi Willd.	14	16	7	0·4	0·2	0·1
Mnium affine Bland	14	8	0	0·2	0·1	—
M. cuspidatum (L.) Leyss.	35	25	20	3·0	2·5	1·5
Orthotrichum leiocarpum B. and S.	0	8	0	—	0·1	—
O. obtusifolium Schrad.	35	25	0	2·0	1·0	—
Pohlia nutans (Schreb.) Lindb.	14	8	20	0·1	0·1	0·2
Polytrichum juniperinum Willd.	14	8	3	0·2	0·2	0·1
Ptilium Crista-castrensis (L.) De Not.	14	8	7	0·2	0·1	0·1
Pylaisia polyantha (Schreb.) B. and S.	70	80	90	5·0	10·0	10·0
Rhytidiadelphus triquetrus (L.) Warnst.	7	0	0	0·2	—	—
Sphagnum capillaceum	14	0	0	0·2	—	—
Stereodon Lindbergii (Mitt.) Warnst.	0	8	0	—	0·1	—
Thuidium recognitum (Hedw.) Lindb.	28	16	3	1·5	0·5	0·1
Tortula mucronifolia Schwaegr.	0	0	3	—	—	0·1
Biatoriana spp. (incl. B. Jungermanniae)	0	8	10	—	0·1	0·1
Cladonia spp.	14	8	20	0·1	0·1	0·1
Parmelia glabra Nyl.	7	0	0	0·1	—	—
P. sulcata Tayl.	7	0	0	0·1	—	—
Peltigera spp.	14	8	24	0·1	0·1	0·2
Physcia stellaris Nyl.	0	8	10	—	0·1	0·2
P. hispida	0	0	7	—	—	0·1
Placodium cerinum Hepp.	7	8	30	0·1	0·1	1·0
Usnea florida var. hirta Ach.	7	0	0	0·1	—	—
Xanthoria lychnea Th. Fr.	7	0	0	0·1	—	—

As already indicated, the two chief dominants of the poplar vegetation are the aspen and the balsam poplar. The associated vegetation appears, on the whole, remarkably uniform in composition; yet close observation and careful analyses have led to the recognition of two main vegetational types. Since these two types are dominated respectively by the aspen and the balsam poplar, they may be named the Aspen and the Balsam Poplar consociations. Recognition of these consociations has rested upon the following considerations:

(1) Each type possesses a single dominant.

(2) Each is characterised by habitat peculiarities (p. 389).

(3) Each contains a number of characteristic species (p. 399).

Since a large number, approximately 25, of the leading species of the poplar vegetation are important constituents of both of the types, and since the number of characteristic species in each type is relatively small, we consider that these types should be regarded as consociations rather than as associations. Therefore, we regard the entire poplar vegetation of our area as an association, and recognise, in this association, two consociations. These occupy extensive areas in practically pure form and are also found intermixed in various proportions. As shown in Table III, our studies have included numerous stands in which the two poplars are co-dominant, i.e. the two consociations intermixed.

The poplar association consists of five rather well-defined layers or strata, viz. (1) taller trees, forming a practically continuous canopy; (2) smaller trees and larger shrubs, an intermittent layer, usually poorly developed in the aspen consociation (Pl. XXIII, phot. 4); (3) lower shrub layer, often sparse, and usually inconspicuous, especially in late summer, when somewhat obscured by members of the next layer; (4) taller herbs, often an almost continuous stratum, and quite prominent in the latter part of the growing season; (5) lower herbs, including mosses and lichens, forming a carpet, which at times is continuous, especially in the balsam poplar consociation. In the aspen consociation, this stratum is usually not well developed, the ground being commonly either bare or covered by a layer of partially decomposed leaves.

The methods employed to determine the frequencies of the various species may be outlined here. In many of the stands studied, quadrats (1 metre square) were laid out at regular intervals in typical parts of the stand, and the frequencies of the species in the quadrats recorded. These records had reference to cover degree, that is, they represented our estimate of the ground area occupied in vertical projection by the different species. Each of the five strata in the vegetation was thought of as having a possible total cover degree of 100 per cent., and the frequencies of the species in each stratum were estimated on that basis. The frequencies thus obtained for each species were then averaged to give the frequency index of the species in the stand as a whole. In certain of the stands critically studied, quadrats were not laid out, but frequency indices were determined by close observation, having in mind earlier experiences with quadrat estimates. Incidentally we may note that these percentage frequency indices bear relationship to familiar frequency symbols and scale degrees as follows:

Percentage				Scale
0·1– 0·5	Very rare to rare	v.r.– r.		
0·5– 2	Occasional	o.		1
2 – 5	Scattered (rather common)	s.		
5 – 15	Frequent (quite common)	f.		2
15 – 30	Abundant	a.		3
30 – 50	Very abundant or co-dominant	v.a., c.d.		4
50 –100	Dominant	d.		5

Having thus obtained frequency indices for the various species in numerous stands of each of the vegetational types, we then derive frequency values for each consociation as a whole. This is done by adding together, for each species, the frequency indices of the various stands of the consociation and then dividing by the total number of stands, the average obtained representing the frequency index of the species in the consociation (Table III).

This method of combining the frequency value of a species in a sample of a community with the constancy value of the species in the community as a whole is not a new one. As reported in a recent paper by Nichols (7), Nordhagen has used essentially the same analysis in his investigation of the

Phot. 3. Balsam Poplar-Aspen community with vigorous
young white spruce.

Phot. 4. Aspen consociation showing herb strata
well developed; trees 32 years old.

MOSS—THE VEGETATION OF ALBERTA. IV. THE POPLAR ASSOCIATION AND
RELATED VEGETATION OF CENTRAL ALBERTA

Phot. 5. *Elaeagnus-Symphoricarpos* society in Parkland, *Elaeagnus* forming the upper layer, and *Symphoricarpos* the lower; surrounded by Prairie vegetation.

Phot. 6. Young aspen grove, 15 years old, with border dominated by *Symphoricarpos occidentalis*; Prairie vegetation in foreground.

MOSS—The Vegetation of Alberta. IV. The Poplar Association and Related Vegetation of Central Alberta

vegetation of the Sylene region in Norway. The index derived is designated the *absolute constancy value*, a term which appears to be the equivalent of what we prefer to name simply the *frequency index* of the species in the community.

In Table III the figures representing constancy values give a clue to the species that predominate in the poplar association as a whole and also to the species that characterise each of the consociations. A species with a high constancy value for one consociation and a very low value for the other consociation may be regarded as a "characteristic" species of the first consociation. In general, however, more reliable information concerning the leading and characteristic species is provided by the frequency index values, which, as already explained, combine constancy values and values for abundance or frequency (in terms of cover degree). The values for mixed stands are also significant, for they provide a check upon conclusions suggested by the frequency indices for the consociations. As a rule, the value for balsam poplar-aspen stands is intermediate between the values for the consociations, as might be expected; but, in some cases, e.g. *Aster Lindleyanus, Thalictrum venulosum*, it is markedly higher. Such apparent discrepancies as the last may be due to errors in field work or in calculation; however, we are inclined to believe that these results have ecological significance, namely, that those species whose frequency indices are much higher in mixed stands than in either consociation usually reach their best development in habitats which are intermediate in certain important respects between typical balsam poplar and aspen habitats.

A study of the analysis shown in Table III, supplemented by field observations not included in the table, has led to the following conclusions: (1) Of some 217 species recorded for the poplar vegetation only about 50 vascular plants and a very few mosses are to be regarded as important constituents; these are listed in Table IV. (2) Since a large number, approximately one-half, of the leading species and species groups of the poplar vegetation are abundantly represented in both balsam poplar and aspen types, and since the number of species characteristic of each type is considerably smaller, we are led to regard the entire poplar vegetation of our areas as an association and each of the types as a consociation. (3) The balsam poplar consociation includes 148 vascular plants of which about 40 are important members, and about 29 mosses and lichens, of which only some 4 mosses are of common occurrence. (4) The aspen consociation, in spite of its wide range, both geographical and environmental, includes only 122 species of vascular plants, of which about 35 have a high frequency, and 24 mosses and lichens, of which not more than 2 mosses are abundantly distributed. (5) Of the leading species and species groups in the poplar association (Table IV), approximately one-half are important constituents of both consociations, while of the other half, some 17 are characteristic of the balsam poplar consociation and some 9 are

characteristic of the aspen consociation. (6) As shown in Table IV, a large proportion of the important trees and shrubs are regarded as "characteristic" of one or other consociation, while a much smaller proportion of the leading herbs are "characteristic" in this respect. Apparently, therefore, the trees and shrubs, as a group, have been more markedly affected than the herbs by certain selective environmental factors that characterise the habitats of the two consociations.

Table IV. *Leading species of balsam poplar and aspen consociations.*

	Characteristic of balsam poplar consociation	Characteristic of aspen consociation	Prominent in both consociations
Trees and shrubs	Populus balsamifera Cornus stolonifera Salix spp. Ribes spp. Alnus incana Picea albertiana Lonicera involucrata	Populus tremuloides Symphoricarpos pauciflorus Amelanchier alnifolia Corylus rostrata Prunus spp.	Rosa spp. Viburnum pauciflorum Rubus strigosus Lonicera glaucescens
Herbs	Mertensia pilosa Equisetum spp. Petasites palmata Galium triflorum Mitella nuda Actaea spp.	Aralia nudicaulis Cornus canadensis Maianthemum canadense Schizachne purpurascens	Rubus triflorus Aster Lindleyanus Agropyron spp. Calamagrostis canadensis Fragaria spp. Viola canadensis Linnaea borealis var. americana Galium boreale Pyrola spp. Epilobium angustifolium Bromus ciliatus Lathyrus ochroleucus Thalictrum venulosum Vicia americana Smilacina stellata Solidago spp. Heracleum lanatum Disporum trachycarpum
Mosses	Hylocomium splendens Aulacomnium palustre Orthotrichum obtusifolium Thuidium recognitum		Pylaisia polyantha Mnium cuspidatum

The life forms exhibited by the poplar association are of some interest. Classified according to Raunkiaer's system, the life forms of the 170 species of seed plants occur in the following percentages: phanerophytes 25·8 (mesophanerophytes 2·3, microphanerophytes 10·0, nanophanerophytes 13·5); chamaephytes 1·8; hemicryptophytes 48·2; geophytes 17·1; therophytes 7·0. This result is very similar to that recorded by Gates (4) for the poplar vegetation of northern Michigan; although it may be noted in passing that the floristic composition of the poplar association of Alberta is quite different from that of the poplar association of Michigan. The large percentage of hemicryptophytes is to be expected in our region, but the number of phanerophytes is higher than might be anticipated. The importance of phanerophytes in the poplar association is further emphasised by considering only the dominant and characteristic species, viz. mesophanerophytes 5·2; microphanerophytes

Phot. 7. Parkland; Aspen vegetation on north slopes,
Prairie on south slopes.

Phot. 8. Rolling Parkland, viewed from the south.

Phot. 9. Flat Parkland, partly cultivated; trees mainly
in depressions, Prairie elsewhere.

MOSS—THE VEGETATION OF ALBERTA. IV. THE POPLAR ASSOCIATION AND
RELATED VEGETATION OF CENTRAL ALBERTA

14·0; nanophanerophytes 22·8; chamaephytes 1·8; hemicryptophytes 42·1; geophytes 14·0; therophytes 0. Of interest too is the fact that there are more than twice as many species of phanerophytes in the balsam poplar consociation than in the aspen consociation; this is probably related to differences in water supply in the habitats of the consociations. Finally, it should be pointed out that a life-form "spectrum" for the poplar region as a whole would differ from the "spectrum" of the poplar association as shown above, in certain important respects; for example, the percentage of phanerophytes would be much reduced because of the inclusion of a large number of hemicryptophytes, geophytes, helophytes and hydrophytes from low moor, reed swamp and other associations in the region.

THE PARKLAND OR GROVE BELT.

(a) General description.

As already indicated, the terms "Parkland" and "Grove Belt" are applied, in this paper, to a transition or tension belt which lies between the Poplar Area and the Prairie (Fig. 1). This belt consists of groves of aspens and patches of prairie grassland, more or less uniformly intermixed. In the central part of the belt, these two types of vegetation dominate practically equal areas, the aspen community occupying the more moist and more sheltered situations, the prairie occurring in the drier and more exposed places. Such typical Parkland is illustrated in Pl. XXV, phot. 8, which shows a rolling area viewed from the south with the aspen consociation dominating most of the depressions and north slopes, and prairie vegetation occupying the drier south slopes— a most striking example of the effect of topography upon vegetation. A clearer illustration is presented in Pl. XXV, phot. 7, which shows a knoll viewed from the east with aspen vegetation on the north slope and prairie on the south slope. In areas of this kind the aspen consociation also occurs on northeast and sometimes on east slopes, while prairie usually occupies west slopes. A rather flat area of the Parkland is shown in Pl. XXV, phot. 9. A portion of this area has been brought under cultivation, but much of the treeless portion is dominated by virgin prairie; and the general view presented is typical of much of the Parkland, especially of the south-eastern part, where prairie is more prominent than wooded vegetation.

Near the southern limit of the Parkland, prairie vegetation occupies a large proportion of the region, wooded vegetation being mainly confined to the margins of sloughs, banks of streams and north-facing slopes of deep ravines and river valleys. In these situations, the wooded vegetation may be dominated by poplar, but very often the only trees present are small willows, prevailing species being *Salix petiolaris*, *S. discolor*, *S. bebbiana* and *S. interior* Roulee. Towards the northern and western limits of the Parkland, on the other hand, the aspen consociation comprises the bulk of the natural vege-

tation and prairie vegetation is generally restricted to the steeper and drier southern exposures. In passing, it may be pointed out that prairie vegetation is of occasional occurrence in the Poplar Area, for example, on very dry south-facing slopes of river valleys; also, prairie vegetation tends to invade parts of the Poplar Area that have been drained, frequently burned and kept clear of trees for a period of years, for example, roadsides.

(b) *The prairie vegetation.*

The Prairie is a complex formation dominated by numerous grasses which are variously intermixed or grouped. In Alberta, the Prairie consists of two rather well-defined communities which we name the Northern Prairie and the Southern Prairie. Whether these communities should be regarded as associations is a question requiring further investigation. Although there is a broad transition belt between the Northern and Southern Prairies and, although there occur "islands" or "out-liers" of each, one within the other, yet we may represent, in a general way, the areas occupied by them, as in Fig. 1. It will be noted that the Southern Prairie coincides closely with the Brown Soil belt, while the Northern Prairie occupies the greater part of the Dark Brown Soil belt.

The dominant and certain subsidiary species of the Prairie are shown in Fig. 3, in which the black bands represent our conception of the occurrence and relative abundance of the different forms. It should be pointed out that we are here considering only typical prairie vegetation, such as forms the natural cover of a very large proportion of the region, and are ignoring the vegetation of various special habitats occurring within the prairie, for example, sandy areas, alkali flats, coulées and other depressions. The leading grasses of the Southern Prairie vegetation are *Bouteloua gracilis* (H.B.K.) Lag., *Stipa comata* Trin. and Rup., *Agropyron Smithii* Rydb. and *Koeleria gracilis* Pers. (the latter may perhaps be more properly regarded as a member of the Northern Prairie community); while grasses of secondary importance include *Stipa viridula* Trin., *Poa* spp., *Agropyron dasystachyum* (Hook.) Scribn. and certain other species of *Agropyron*.

Clarke (13), in a paper that came to hand after the present paper was accepted for publication, gives the most reliable account yet available of the vegetation of the Southern Prairie or Short Grass Plains of Western Canada. Clarke regards *Agropyron Smithii* as a somewhat less important constituent and *Poa* spp. as considerably more important members of the Southern Prairie than is reported in the present paper.

The leading species of the Northern Prairie region include several of those that are prominent in the Southern Prairie, notably *Koeleria gracilis*, *Stipa* spp., *Agropyron* spp. and *Bouteloua gracilis,* and, in addition the following: *Festuca scabrella* Torr., *Avena Hookeri* Scribn., *Agropyron tenerum* Vasey and *A. Richardsoni* Schrad. and *Poa interior* Rydb. Grasses of secondary

importance are *Muhlenbergia squarrosa* (Trin.) Rydb., *Danthonia intermedia* Vasey, *Agrostis hyemalis* (Walt.) B.S.P., *Bromus Porteri* (Coult.) Nash, and several species of *Poa*, of which *P. pratensis* L. and *P. palustris* L. have become dominant in many places, especially in Parkland areas where the natural vegetation has been more or less destroyed, for example, on roadsides.

As indicated in Fig. 3, the chief grasses of the Northern Prairie vegetation may be arranged in approximate order of importance as follows: *Koeleria gracilis, Festuca scabrella, Stipa comata, Agropyron tenerum, A. Richardsoni,*
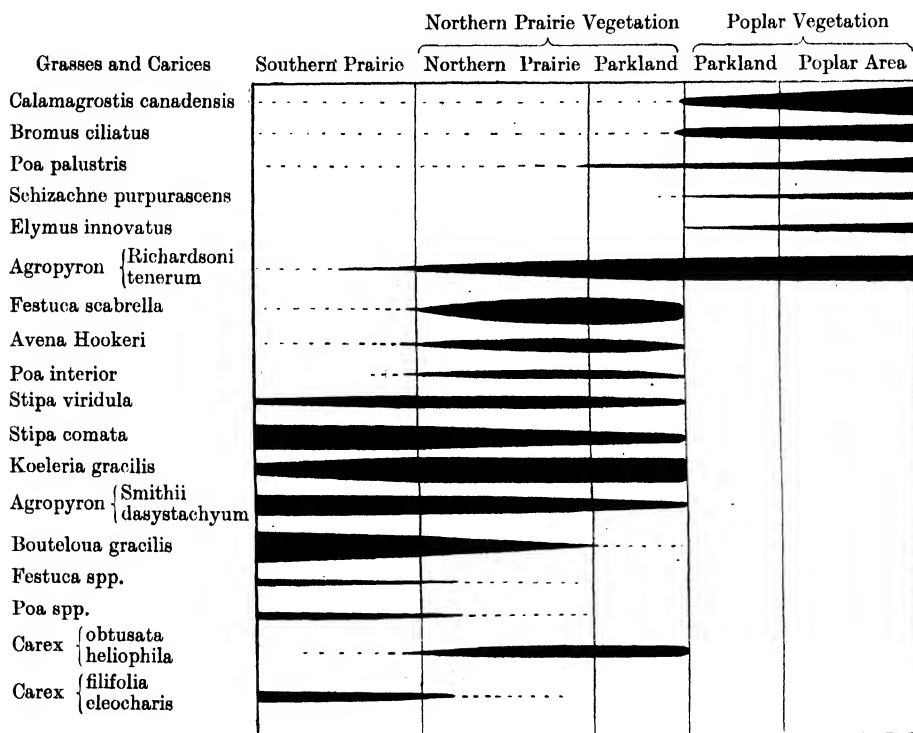
FIG. 3. A graphical representation of the occurrence and relative abundance of leading grasses and sedges in various regions and communities.

A. dasystachyum, A. Smithii, Avena Hookeri, Stipa viridula, Bouteloua gracilis and *Poa interior*. There is, however, some doubt whether certain of these grasses (namely, *Bouteloua gracilis, Agropyron Smithii, A. dasystachyum,* and perhaps also *Stipa* spp.) are to be regarded as important constituents of the Northern Prairie community; they are usually abundant or dominant in the more xeric situations of the Northern Prairie region and may perhaps be properly thought of as "islands" of the Southern Prairie community in the Northern Prairie region. Associated with the grasses in the Northern Prairie are certain small sedges, of which *Carex obtusata* Lilj. and *C. heliophila*

Mackenzie are often abundant. Other common and characteristic species of the Northern Prairie community are as follows: *Cerastium arvense* L., *Pulsatilla ludoviciana* (Nutt.) Heller, *Sieversia ciliata* (Pursh.) G. Don., *Comandra pallida* DC., *Selaginella densa* Rydb., *Symphoricarpos occidentalis* Hook., *Gaillardia aristata* Pursh., *Achillea lanulosa* Nutt., and species of *Aster, Artemesia, Antennaria, Solidago, Helianthus, Grindelia, Chrysopsis, Rosa, Potentilla, Fragaria, Androsace, Thermopsis, Astragalus, Oxytropis, Petalostemon, Pentstemon, Heuchera, Linum, Arabis, Anemone* and *Zygadenus.*

The relationship between Northern Prairie and Southern Prairie vegetation may be further considered by reference to Fig. 3. It will be observed that as one passes from one type of prairie to the other, practically all of the dominant grasses show either a marked decrease or increase in abundance. A similar relationship holds for various subsidiary grasses, for certain carices, and also for numerous species not included in Fig. 3. These features, taken in conjunction with certain facts regarding the habitat relationships and grouping of the leading species (referred to in the preceding paragraph), appear to provide a sound basis for the recognition of Northern and Southern Prairie communities. Of these, it is the Northern Prairie that usually comes into immediate conflict with the poplar association and it is this community therefore which is of particular interest in the present discussion. By way of summary, we may state tentatively that the Northern Prairie community is composed of the dominant grasses, *Koeleria gracilis, Festuca scabrella, Agropyron Richardsoni, A. tenerum* and *Avena Hookeri*, and numerous secondary species, including various grasses, carices and other common and characteristic species already noted.

(c) *Ecotone between prairie and poplar vegetation.*

The Parkland has already been described as a broad transition or tension belt consisting of patches of poplar and prairie vegetation. This transition belt contains within it thousands of true tension lines or ecotones, these occurring wherever poplar and prairie communities meet. Photographic illustrations of tension lines may be referred to here. In Pl. XXV, phot. 7 a narrow ecotone extends along the top of the elevation between the prairie vegetation on the south slope and the aspen consociation on the north slope, and consists of representatives of the two competing communities. Leading forms include various grasses and such shrubs as *Symphoricarpos, Rosa, Prunus, Elaeagnus argentea* and *Shepherdia canadensis*. The ecotone also extends along the east face and again along the west face of the elevation and in these situations is usually a rather broad band. In Pl. XXIV, phot. 6 is shown a typical ecotone—a narrow belt, dominated by the "wolfberry," *Symphoricarpos occidentalis*, bordering the aspen grove. The wolfberry extends into the prairie, smothering the grass, and is followed by the aspen, shoots of which come up in the wolfberry belt, eventually becoming dominant there. In many situa-

tions the aspen vegetation thus tends to invade and to succeed the prairie vegetation; and the border of the aspen grove then becomes composed of trees that are considerably younger than those of the main body of the stand. Determinations of the ages of trees in the border of one such grove indicated that the rate of advance of the trees during the last 12 years has been about 15 cm. per year. It should be pointed out here that the occurrence of younger trees on the border of a grove is not always to be explained as above, but rather may be the consequence of one or more burnings of the marginal part of the grove, the younger trees having sprung from the underground parts of the burned trees. A situation of this kind is usually recognisable by the fact that the trees of the greater part of the bordering belt are of the same age; whereas, in a belt formed as a result of invasion of the prairie, the trees show a progressive increase in age from the periphery inwards.

This marked tendency for the aspen consociation to invade and replace prairie vegetation is convincingly illustrated in many parts of the Parkland; and, in the absence of burning, succession in this direction would soon produce considerable extension of woodland. That burning has been effective in stemming the advance of trees is clearly shown by certain areas investigated. On the other hand, where fires have not occurred or have been infrequent, for several years, as is usually true of regions that have been for some time settled and in part under cultivation, the trees have made marked advances upon the prairie. Early settlers of the Parkland region assert that groves are now more numerous and more extensive than they were a number of years ago.

There seems to be good reason therefore to conclude that fire has been a very important factor in preventing expansion of the aspen consociation in the Parkland, and probably too in limiting the southern extension of the Parkland area. During past centuries the frequency of burning has doubtless fluctuated very considerably (p. 391). In very dry periods frequent fires no doubt invaded the region, burning off aspen groves and possibly killing some of them as a whole or in part. This appears to have been the situation in the Parkland and also in the southern part of the Poplar Area about 1890 when many of the early settlers arrived, and may be the foundation of the popular belief that various regions now well wooded were at one time prairie. During the subsequent wet period, numerous aspen groves appeared in the region, possibly from seed, but more likely, in the main, from roots that had survived the dry period and the ravages of frequent fires.

While fire is considered to be the chief factor responsible for checking the invasion of prairie by the aspen, certain other factors are at times quite effective. The snowshoe rabbit, *Lepus americanus phaeonotus* Allen, by girdling young aspens, exerts a marked effect, at least during periods when this species is at a maximum. Bird (1) states that "the aspen would advance much more quickly on to the prairie, if it were not for the rabbits." The buffalo, *Bison bison* L., doubtless an important factor in the past, ceased to be effective some

50 years ago, when the last of the great wild herds were slaughtered. In recent years, man has interfered greatly with the development and extension of aspen groves by cutting trees, by setting fires, by cultivating areas adjoining groves and by draining certain areas. On the whole, however, and excluding from consideration regions that are now largely under cultivation, man has tended to shift the balance in favour of aspen vegetation, because he has prevented the frequent occurrence of widespread burning.

The striking correlation, already noted, between the occurrence of the two types of Parkland vegetation and the topography of the region appears to be a consequence of three interrelated circumstances, namely:

(1) Hill tops and south-facing slopes, being generally hot, dry situations, are suited to the development of prairie vegetation but do not favour the invasion and growth of trees; whereas, depressions and north-facing slopes, being much less xeric, favour the growth of trees and the consequent exclusion of prairie grasses.

(2) Burning is common in the drier situations but much less frequent in the more moist habitats, with the result that invasion of prairie vegetation by trees is counteracted; therefore, restriction of the two vegetational types to their characteristic habitats tends to be maintained.

(3) Ecesis of the aspen probably occurs very rarely in the drier situations, but not infrequently in the more moist places. This subject is considered at length in the following paragraphs.

At some time in the past, whether in comparatively recent years or many centuries ago, the thousands of isolated aspen groves of the Parkland must have been initiated by seed. The question of the time factor involved here may be elucidated in the future by a critical study of the soils on north and south slopes. At present we are inclined to believe that groves of trees have been abundant in the greater part of the Parkland for many years but not for many centuries. Even the Poplar Area seems not to have been dominated by trees for a very long period of time. For, as noted in the earlier part of the paper, the soils of most of the Parkland and Poplar Areas are of the grassland rather than the wooded type. Furthermore, with the exception of the black soils in the extreme northern and western parts of the Poplar Area, these soils show only a slight transformation of the kind expected in grassland soils that had been wooded for many centuries.

Establishment of the aspen in grassland appears to be dependent upon the following conditions: (1) The transfer of viable seed; how far aspen seed may be transported in a viable condition is problematical. (2) Local climatic and edaphic conditions favourable to the germination of the seed and the establishment of seedlings, conditions that may rarely obtain, at least while the seed is still viable. Although no measurements have been made, there is undoubtedly a great difference in this respect between north and south slopes, the latter subject to direct insolation, being much hotter and drier. (3) An

open prairie community, such as is likely to occur on steeper slopes, as a consequence of erosion. Doubtless, there are occasional years in which all of these conditions are fulfilled and when the aspen may, therefore, become locally established in the prairie community, especially in depressions and on north and north-east slopes.

Another way in which aspens may become established in the prairie will now be considered. Within the prairie community of the Parkland there occur numerous stands of the wolfberry, *Symphoricarpos occidentalis*. In the southern part of the Parkland these stands commonly occupy shallow depressions and northern exposures, while farther north they occur in drier habitats, often on hillocks. On lighter soils, *Symphoricarpos* is usually accompanied by another shrub, the silverberry, *Elaeagnus argentea*. Not uncommonly, these shrubs occur as co-dominants, forming two quite distinct layers, the greyish silverberry projecting far above the deep green wolfberry (Pl. XXIV, phot. 5). These communities, the first dominated by *Symphoricarpos*, the second by *Symphoricarpos* and *Elaeagnus*, may be regarded as societies or possibly as associes. Accompanying species include *Rosa* spp., *Rubus strigosus*, *Galium boreale*, *Lathyrus ochroleucus*, *Solidago* spp., *Anemone* spp., *Agropyron* spp. and other grasses. According to Bird (1), who has recently studied the eastern part of the Canadian Parkland, these shrub communities have become established in grassland as a consequence of the activities of certain animals; and our own observations point to the same conclusion. There is also considerable evidence that the shrub communities are, in some cases, succeeded by the aspen consociation, the aspen being initiated by seed. Bird claims that succession along these lines is largely due to the activities of the following animals: "gophers" or ground squirrels, including Richardson's ground squirrel, *Citellus richardsoni* and the pocket gopher, *Thomomys talpoides rufescens*; the badger, *Taxidea taxus*, the chief predator of *Citellus*; and the pine grosbeak, *Pinicola enucleator*. According to Bird, gophers and badgers throw up mounds of earth that choke out the grass, thus enabling *Elaeagnus* and *Symphoricarpos* to gain a foothold, seeds of the latter shrub being distributed in large numbers by the pine grosbeak. In the comparatively loose earth and sheltered conditions of *Symphoricarpos* and *Symphoricarpos-Elaeagnus* stands, aspen seedlings may become established.

THE WHITE SPRUCE ASSOCIATION.

(a) *Floristic composition.*

As noted above, the white spruce, *Picea albertiana*, occurs rather commonly in the poplar association, especially in the balsam poplar consociation. In certain, mainly small, areas of the poplar region spruce is dominant and has a characteristic accompanying vegetation. This white spruce association is usually found in habitats similar to those occupied by the balsam poplar

consociation. It is not surprising, therefore, that these two communities are found to have many species in common. In this connection it may be noted that the dominants of the two communities commonly occur more or less equally intermixed (Pl. XXII, phot. 2); and the vegetation of such spruce-poplar stands is composed of species that characterise both communities.

Only a brief description of the composition of the white spruce association will be given here. The following list is by no means complete but will serve to give some idea of the floristic composition of the association.

Taller trees.

Picea albertiana	d.	P. tremuloides	r.—o.
Populus balsamifera	o.—f.	Betula papyrifera	r.—o.

Smaller trees and larger shrubs.

Cornus stolonifera	o.—f.	Alnus spp.	o.
Salix spp.	o., l.a.	Amelanchier alnifolia	o.

Smaller shrubs.

Rosa spp.	o.—f.	L. glaucescens	o.
Ribes spp.	o.—f.	Symphoricarpos pauciflorus	r.—o.
Viburnum pauciflorum	o.—f.	Vaccinium Vitis-Idaea	r.—o.
Rubus strigosus	o.	Ledum groenlandicum	r.—o.
Lonicera involucrata	o.	Rhamnus alnifolia	r.

Mosses and lichens.

Hylocomium splendens	a.	Eurynchium strigosum	o.
Hypnum Schreberi	a.	Mnium cuspidatum	o.
Ptilium Crista-castrensis	f.	Aulacomnium turgidum	o.
Rhytidiadelphus triquetrus	o.—f.	Oncophorus Wahlenbergii	r.
Thuidium recognitum	o.—f.	Thuidium Blandowii	r.
Camptothecium nitens	o.—f.	Climacium dendroides	r.
Aulacomnium palustre	o.—f.	Sphagnum Girgensohnii	r.
Polytrichum juniperinum	o.—f.	S. capillaceum	r.
Dicranum undulatum	o.—f.	Peltigera apthosa	f.
Dicranum spp.	o.—f.	Cladonia spp.	o.—f.
Pylaisia polyantha	o.—f.		

Herbs.

Linnaea borealis	f., l.a.	Agropyron spp.	o.
Equisetum arvense	f., l.a.	Bromus spp.	o.
E. scirpoides	f.	Smilacina stellata	o.
E. pratense	o.	Thalictrum spp.	o.
Calamagrostis canadensis	f., l.a.	Actaea spp.	o.
Cornus canadensis	f.	Fragaria spp.	o.
Mitella nuda	f.	Lathyrus ochroleucus	o.
Rubus triflorus	f.	Moneses uniflora	o.
R. arcticus	o.	Peramium ophioides	o.
Pyrola secunda	o.—f.	Habenaria spp.	o.
P. asarifolia	o.—f.	Orchis rotundifolia	o.
P. chlorantha	o.	Corallorrhiza spp.	r.
Maianthemum canadense	o.—f.	Circaea alpina	r.
Petasites palmata	o.—f.	Oxalis stricta	r.
Aster spp.	o.—f.	Aspidium spinulosum	r.
Viola spp.	o.—f.	Cystopteris fragilis	r.
Mertensia pilosa	o.—f.	Chrysosplenium iowense	r.
Aralia nudicaulis	o.—f.	Schizachne purpurascens	r.
Galium triflorum	o.	Heracleum lanatum	r.
Carex concinna	o.	Disporum trachycarpum	r.
C. saltuensis	o.	Comandra livida	r.
C. eburnea	o.	Parnassia palustris	r.
Carex spp.	o.		

The smaller trees and the shrubs are not numerous and as a rule are sparsely scattered. The ground flora is variable and generally patchy. Where the spruce forms a close canopy, thus excluding strong sunlight, there usually occurs a continuous thick carpet, consisting of various mosses, notably the first three species listed above. Where the stand is more open, this characteristic "feather" moss stratum is not so well developed, but various other mosses may be locally abundant; also, certain herbs, especially *Linnaea borealis*, *Equisetum* spp. and *Calamagrostis canadensis*, are commonly abundant in these parts of the association.

(b) *Ecotone between white spruce and poplar associations.*

Competition between these associations is primarily a struggle between the dominants, white spruce and poplar. These species appear to thrive in similar situations. There is considerable evidence that spruce would grow on the various sites that produce fairly good growth of poplar (i.e. with a site index of over 50). This statement applies not only to the balsam poplar but also to the aspen. The comparatively rare occurrence of spruce in aspen stands, at least in northern and western parts of the poplar region, is believed to be a consequence of frequent burnings of these stands. If, during recent centuries, fires had not occurred, spruce would undoubtedly have extended much farther south and east in the Poplar Area (Fig. 1) and would probably have become dominant in at least part of that region. In other words, white spruce appears to be the climax species of a considerable part of the poplar region.

It may be noted here that certain earlier investigators of our region have expressed an opinion similar to that stated in the preceding paragraph. White (9), for example, points out that the aspen makes an excellent nurse tree for the spruce and claims that if fires are controlled the poplar will gradually be replaced by spruce. On the other hand, Bird (1) believes that the aspen is climax over a large area in Manitoba and Saskatchewan. However, the area to which Bird refers seems to be comparable in most respects with the Parkland and extreme southern part of the Poplar Area of Alberta (Fig. 1). There is indeed some doubt whether, in these areas, spruce would replace aspen, even in the absence of burning; therefore, we are inclined to regard the aspen consociation as the climax vegetation of the Parkland and also of the more southern parts of the Poplar Area.

There is abundant evidence that ecesis of white spruce occurs in poplar stands of various ages, also in bushland that has been frequently burned in recent years, and even in low, moist grassland. The establishment of vigorous young spruce in a somewhat open poplar stand is shown in Pl. XXIII, phot. 3. Observation made in regions where isolated seed trees occur showed that young white spruce are usually of common occurrence in the immediate vicinity of the parent tree but are rarely found beyond a radius of about

100 metres. Spruce that start in a young poplar stand usually make quite slow growth for many years, apparently due to shading by the rapidly growing poplar. But, as the poplar stand thins out with advancing age, the suppressed and seemingly stunted spruce grow rapidly and may eventually over-top the surrounding poplar. This situation is commonly met with in stands of 70 years and older (Pl. XXII, phot. 1). In stands of this kind young spruce usually start in large numbers, and are likely to make rapid growth because of the incomplete dominance of the poplar. In this way, therefore, the white spruce may succeed the poplar; and, under the dense shade of the spruce the characteristic subsidiary species of the white spruce association gradually replace those of the poplar association.

Counteracting this natural tendency of the spruce to supersede poplar are at least two factors, namely, burning and snowshoe rabbits, of which the former is undoubtedly the major one. Spruce trees do not produce seed in quantity until they are about 35 years old; therefore, one can readily account for the scarcity of spruce in a region whose natural vegetation has been in large part burned off approximately every 20 years. Rabbits injure the leaders of young spruce and so may effectively retard development of these trees. Only after trees have reached a height of about 4 ft., thus bringing their leaders well above snow-level, are they in a position to escape serious damage on the part of rabbits.

Successional relationships.

The poplar-prairie and poplar-spruce ecotones have already been discussed. Consideration will now be given: (1) to the perpetuation of the poplar association in the absence of burning; (2) to effects of burning, cutting and grazing upon the poplar association; (3) to hydroseres and xeroseres of the poplar region, with a view to indicating the place occupied by the poplar association in these seres.

Perpetuation of the poplar association in the absence of burning appears to be of infrequent occurrence in our region. Old poplar stands (100 years or more in age) showing no indication of burning are comparatively rare; furthermore, these stands usually occur in rather low, moist habitats. With the dying of the old poplars numerous young poplars appear, but not quickly enough or in sufficient numbers to maintain the dominance of poplar in the community. On the contrary, various other woody plants increase greatly in abundance, becoming locally dominant, thus producing a patchy community. Also, a number of herbaceous species, notably *Calamagrostis canadensis*, become quite abundant. In the more moist situations, the dominant trees and shrubs usually include *Salix myrtillifolia, S. discolor, Cornus stolonifera, Viburnum Opulus, V. pauciflorum* and *Alnus incana;* while in drier places, the dominant woody species are likely to be *Salix bebbiana, Viburnum pauciflorum, Corylus rostrata, Prunus* spp., *Symphoricarpos* spp. and *Rosa* spp.

Little information appears to be available regarding later stages in development of these stands; but, the probability is that dominance on the part of shrubs and small trees is only temporary and that young poplars soon become dominant throughout. Presumably, a poplar stand thus initiated would contain trees of various ages. To what extent these trees arise from roots of old trees, and to what extent from seed, is a problem requiring further investigation.

A poplar stand that has been burned off is usually soon replaced by a stand of young trees, with only a temporary alteration occurring in the composition of the associated vegetation. Following a fire certain plants, including *Rosa* spp., *Rubus* spp., *Symphoricarpos* spp., *Corylus rostrata*, *Epilobium angustifolium*, *Aster* spp., *Solidago* spp., *Agropyron* spp., *Bromus ciliatus* and *Calamagrostis canadensis*, become dominant; but, after two or three years, these species are suppressed by the young poplars and there is a gradual return to the original composition of the community. Cutting of a poplar stand produces essentially the same results. Where burning has been quite severe, to the extent of destroying considerable humus and injuring underground parts of poplars and various other species, return to the original type of vegetation is greatly delayed. Repeated burnings at short intervals usually have this effect. The temporary vegetation of these situations is usually patchy, various of the species noted above being locally abundant or dominant. There also occur a number of species that do not belong to the poplar association or are of rare occurrence in that association; some of the more common of these are *Aster umbellatus pubens*, *A. conspicuus*, *A. modestus*, *A. laevis*, *Monarda menthaefolia*, *Agastache anethiodora*, *Castilleja* ? *rhexifolia* and *Carex siccata*. The last species is a common dominant on dry, south-facing slopes that have been frequently burned; in the absence of burning it would undoubtedly be replaced by shrubs and grasses, and these would eventually be dominated by aspens. Where grazing follows severe burning of poplar stands, the natural succession to poplar may be delayed indefinitely; indeed, there commonly arise shrub, sedge or grass communities which are practically stable under the artificial conditions imposed. Such communities (socies or associes) may be dominated by *Symphoricarpos occidentalis*, *Salix petiolaris*, *Carex siccata*, *Poa palustris*, *P. pratensis* or *Koeleria gracilis*. Communities dominated by these grasses are common on roadsides and elsewhere in the poplar region, and have doubtless arisen as a consequence of frequent burning, combined with considerable grazing, mowing and drainage of these areas.

Hydrarch successions from lakes and sloughs include a number of reed-swamp and low-moor associes, the last of the low-moor series usually being a *Salix-Calamagrostis canadensis* associes (6). The latter is quite a prominent feature of the landscape in many parts of the poplar region, although it has often been variously altered in aspect and composition due to man's activities. This associes is in turn succeeded by the poplar association. The following

list will serve to give an approximate idea of the composition of the *Salix-Calamagrostis canadensis* associes.

Salix petiolaris	a.	Aulacomnium palustre and other mosses	f., l.a.
S. discolor	f.	Carex prairea	o., l.a.
S. myrtillifolia	f.	C. praegracilis	o., l.a.
S. balsamifera	f.	C. utriculata	o.
S. maccalliana	f.	C. atherodes	o.
S. planifolia	o.	Rubus arcticus	o.
Ribes spp.	f.	R. triflorus	o.
Cornus stolonifera	f.	Scutellaria galericulata	o.
Alnus incana	f.	Parnassia palustris	o.
Lonicera involucrata	o.	Petasites sagittata	o.
Rubus strigosus	o.	Stellaria spp.	o.
Betula glandulosa	o.	Stachys scopulorum	o.
Calamagrostis canadensis	a.	Caltha palustris	o.
C. inexpansa	o., l.a.	Erigeron philadelphicus	o.
Poa palustris	f., l.a.	Galium spp.	o.
Bromus ciliatus	f.	Ranunculus cymbalaria	o.
Agropyron Richardsoni	f.	Epilobium angustifolium	o.
Agrostis hyemalis	f.	Aster junceus	o.
Juncus spp.	f.	A. puniceus	o.

Where succession is from streams rather than from lakes and sloughs, the willow, *S. interior*, is usually one of the dominants. As conditions in the *Salix-Calamagrostis canadensis* associes become drier, certain species disappear and others, notably the poplars, invade the associes. Eventually the poplars dominate there and the poplar association becomes established.

The xerarch successions in sandhill areas of the poplar region are not easily determined because frequent burnings have prevented development of the more advanced stages. The jackpine, *Pinus Banksiana* Lamb., is the common dominant, due mainly to the fact that this species is much more successful than aspen and white spruce in overcoming the consequences of frequent and severe burning. As Dowding (**2**) has shown, there is considerable evidence that the natural succession of these sandy areas is either to the white spruce or to the poplar association. The probability is that many of the sandy areas invaded and dominated by poplar would eventually become dominated by white spruce. However, further investigation is required to elucidate the relationships between pine, spruce and poplar communities of these areas.

Where white spruce rather than pine dominates on drier parts of sandhills, as is true of an area near Edmonton, the accompanying vegetation is essentially like that associated with pine in similar situations (**2**). Numerous young spruce occur beneath the parent trees, indicating that the community is self-perpetuating under prevailing conditions. Characteristic species accompanying the spruce include: *Arctostaphylos Uva-ursi* (L.) Spreng., *Vaccinium canadense, Carex siccata, Festuca ovina* L., *Oryzopsis pungens* (Torr.) Hitchc., *Equisetum hyemalis* L., *Erigeron glabellus* Nutt., *Artemesia caudata* Michx., *Hieracium canadense* Michx., *Viola adunca* J. E. Smith, *Pulsatilla ludoviciana* (Nutt.) Heller, *Comandra pallida* DC., *Cladonia* spp., *Peltigera* spp., *Polytrichum piliferum, Ceratodon purpureus, Selaginella densa, Rosa acicularis, Amelanchier*

alnifolia, Rubus strigosus, Prunus spp., and *Populus tremuloides*. The last species is represented by scattered individuals, very stunted in appearance. This type of spruce community may be named a white spruce-heath associes. It is of rare occurrence in the poplar region, and obviously is very different in composition from the white spruce association described above as an important climax type.

Where aspen dominates on very sandy areas, the accompanying vegetation is quite different from that of the aspen consociation. In these areas the aspen is usually dwarfed and somewhat sparsely scattered, the open parts of the stand often having a ground cover of mosses, lichens, sedges, grasses, ericads or juniper. Leading species with the aspens include: *Rubus strigosus, Rosa* spp., *Symphoricarpos* spp., *Elaeagnus argentea, Juniperus horizontalis* Moench., *Arctostaphylos Uva-ursi, Vaccinium Vitis-Idaea, V. canadense, Elymus innovatus, Oryzopsis pungens, Festuca* spp., *Agropyron* spp., *Calamovilfa longifolia* (Hook.) Hack., *Carex siccata, Cornus canadensis, Fragaria* spp., *Pyrola* spp., *Maianthemum canadense, Arenaria laterifolia, Selaginella densa*, and various mosses and lichens. This kind of aspen community may be named an aspen-heath associes. It varies greatly in composition from place to place, and several types or consocies may be distinguished. Of these, the *Arctostaphylos-Juniperus* type is quite common.

In the absence of burning, humus would accumulate in the aspen-heath associes and succession to the aspen consociation would undoubtedly take place. Actually, however, burning has interfered very effectively with succession in this direction. In certain areas, it has had the effect either of maintaining the aspen-heath consocies or of bringing about retrogression to associes characterised by xeromorphic sedges, grasses, mosses and lichens. This is the situation in sandy areas of the Parkland and southern part of the Poplar Area. In northern and western parts of the Poplar Area, however, burning has usually brought about the introduction of pine into aspen-heath and other heath associes.

Summary.

The poplar association comprises a large part of the natural vegetation of central Alberta. This association is characterised by somewhat over 200 species, of which only about 50 vascular plants and a very few mosses are important constituents. Two consociations are recognised in the association; these are the balsam poplar and aspen consociations, the former generally confined to rather moist situations, the latter occurring in drier places and being much more widely distributed in the region. The composition of these communities is set forth in a table showing constancy values and frequency indices of species.

In central Alberta, the balsam poplar rarely exceeds 135 years, the aspen 120 years, in age. On the better sites, these species attain a height of about 27 metres in 70 years.

Poplar stands are almost invariably even aged; this is due to the fact that the trees of a stand start as suckers shortly after a complete burning off of the parent stand. Prevailing ages of older stands in the region are 30–38, 50, 70 and 110 years. These ages give a clue to dates of general burning and hence to periods when dry climatic conditions prevailed. On the basis of these considerations, there is proposed a hypothesis concerning 20-year climatic cycles.

Northern and western parts of the region have soils of the grey or wooded type, while central and southern parts are characterised by soils that have developed under a grassland type of vegetation. The evidence provided by soils is, therefore, that much of the poplar region was at one time occupied by prairie; however, the probability is that poplars have dominated in most parts of the area for at least a few centuries.

The aspen consociation tends to invade the prairie to the south and east. This tendency is counteracted mainly by fires, which favour the prairie association and prevent the aspen from occupying the drier situations. As a consequence there occurs between the poplar region and the prairie a broad transition belt, the parkland, consisting of groves of trees in depressions and on north-facing slopes, and patches of prairie vegetation on south-facing slopes and other dry situations. This transition belt contains within it thousands of narrow tension lines or ecotones, these occurring wherever poplar and prairie communities meet. A typical ecotone of this kind is dominated by grasses and shrubs, of which *Symphoricarpos occidentalis* is the most common species.

Consideration is given to the question of the establishment of aspen in grassland by seed, particular reference being made in this connection to the rôle of the shrubs, *Symphoricarpos* and *Elaeagnus*, and certain animals, especially "gophers" and badgers.

A very few species are common to the northern prairie community and the aspen consociation, and of these only two, *Agropyron tenerum* and *A. Richardsoni*, are abundant in both communities. A graphical representation is given of the relative abundance of leading grasses and sedges in southern prairie, northern prairie and aspen communities.

White spruce is almost certainly the climax species of northern and central parts of the poplar regions, while aspen is probably the climax of the southern part of that region and of the parkland. However, succession to spruce has been effectively retarded by certain factors, especially burning. The white spruce association is characterised by a "feather" moss stratum; otherwise it has much in common with the balsam poplar consociation.

Consideration is given to hydroseres and xeroseres of the poplar region, with particular reference to the place occupied by the poplar association in these seres.

REFERENCES.

(1) **Bird, Ralph D.** "Biotic communities of the aspen parkland of Central Canada." *Ecology,* **11,** No. 2, 1930.

(2) **Dowding, E. S.** "The vegetation of Alberta. III. The sandhill areas of Central Alberta with particular reference to the ecology of *Arceuthobium americanum* Nutt." This JOURN. **17,** No. 1, 1929.

(3) **Erlanson, E. W.** "The wild roses of the Mackinac Region of Michigan." *Papers Michigan Acad. Sc., Arts and Letters,* **5,** 1925.

(4) **Gates, F. C.** "Aspen association in northern Lower Michigan." *Bot. Gaz.* **90,** No. 3, 1930.

(5) **Kittredge, J.** and **Gevorkiantz, S. R.** "Forest possibilities of aspen lands in the Lake States." *Univ. Minnesota, Tech. Bulletin,* **60,** 1929.

(6) **Lewis, F. J., Dowding, E. S.** and **Moss, E. H.** "The vegetation of Alberta. II. The swamp, moor and bog forest vegetation of Central Alberta." This JOURN. **16,** No. 1, 1928.

(7) **Nichols, G. E.** "Methods in the floristic study of vegetation." *Ecology,* **11,** No. 1, 1930.

(8) **Peto, F. H.** "Cytological studies in the genus *Agropyron.*" *Canadian Journ. of Research,* **3,** 1930.

(9) **White, J. H.** *Forestry on Dominion Lands.* Commission of Conservation, Ottawa, 1915.

(10) **Wyatt, F. A.** and **Newton, J. D.** "Alberta soil profiles." *Abstracts Proceedings First Intern. Congress of Soil Science.* Fifth Commission, pp. 87–8, 1927.

(11) **Wyatt, F. A.** and **Ward, A. S.** "Fertilizers for wooded soils." *Scientific Agriculture,* **11,** No. 7, 1929.

(12) **Wyatt, F. A., Newton, J. D.** and **Mather, T. H.** "Soil survey of St Ann Sheet." *University of Alberta, Bulletin,* No. 20, 1930.

(13) **Clarke, S. E.** "Pasture investigations on the short grass plains of Saskatchewan and Alberta." *Scientific Agriculture,* **10,** No. 11, 1930.

OBSERVATIONS ON THE VEGETATION OF FINMARK

BY WILLIAM LEACH AND NICHOLAS POLUNIN.

(With Plates XXVI–XXIX and one Figure in the Text.)

THE present account of the vegetation of Finmark is based on notes made by the writers during a visit to that region, in the summer of 1930, as members of the Oxford University Expedition to Lapland. The work carried out, the results of which are about to be described, was of necessity mainly of the nature of a very cursory reconnaissance. This was because circumstances usually rendered impossible the staying in areas that appeared to be especially promising vegetationally, for periods long enough for the making of anything approaching detailed studies. In spite of this, however, a number of observations were recorded which should be of some interest to ecologists unfamiliar with the vegetation of Northern Scandinavia.

It has been considered most convenient to divide this account into three sections dealing respectively with (a) the Vegetation of the Billefjordelv region, (b) the Vegetation of the Lakselv region, and (c) the Vegetation of Central Finmark between the Karasjokka and the Kautokeino rivers. A stay of four days in the first of these regions allowed of the study in some detail of certain aspects of the vegetation. Similarly the somewhat detailed nature of section (b) was rendered possible by a short stay at Lakselv. With regard to section (c) the area is of considerable magnitude and uniformity and is here treated much more cursorily, since it will be separately described, together with the vegetation of Troms, by one of us (N. P.).

BILLEFJORDELV REGION.

The Billefjordelv is a small river which flows north-east and enters the Porsanger Fjord at a point some 35 km. north of Lakselv. A camp was established for four days near this river at a point about 10 km. from its mouth, and at a latitude of about 70° 10′ N. Although most of the detailed observations made here were made within a radius of 5 km. from the camp site, an area of far greater extent was examined in a general way from the hill tops, by means of binoculars.

As far as could be determined, the whole of the rock surface of this region, with the exception of the hill tops, is covered with boulder clay or morain accumulations, and wherever the soil was tested by means of the B.D.H. Universal Indicator, a more or less markedly acid reaction was given.

Considered in a general way, the vegetation of the area is composed of two plant associations, viz. birch forest, dominated almost everywhere by *B. odorata*, and a "heath" type with *Betula nana, Empetrum nigrum*, and

Vaccinium Myrtillus as chief dominants (see Pl. XXVI, phot. 1). Of course these associations show a considerable degree of variation in relation to soil water and exposure. The birch forest occupies the greater part of the valleys and more sheltered areas, and extends up the hill sides to an altitude of about 900 ft. (273 m.). Above this there nearly always occurs the heath type which in turn thins out to almost bare lichen-covered rocks on the exposed summits. Whether this division into two associations is a legitimate one or not, is a debatable point, as for the most part the only constant difference between them is the presence or absence of birch trees.

The Betula odorata *zone.*

Viewed from the vantage point of a hill the birch forest shows a certain amount of variation in appearance owing to local variations in the abundance of trees. In the narrower, more sheltered parts of the valleys, and on slopes where available soil water is abundant the trees often grow in close canopy and in their shade a well-developed phanerogamic ground flora develops, typical lists of species present being given below:

Betula odorata Bechst.	a.—d.	§Anthoxanthum odoratum L.	o.
Sorbus Aucuparia L.	o.—f.	Gnaphalium norvegicum Gunn	o.
Salix glauca L.	o.	Hieracium caesium Fr.	o.
§Juniperus communis	o.	Rumex acetosa L.	o.
Empetrum nigrum L.	v.a.		
Vaccinium Myrtillus L.	v.a.	§Dryopteris Linneana C. Chr.	l.f.
V. uliginosum L.	v.a.	Equisetum sylvaticum L.	f.
§V. Vitis-idaea L.	l.f.	Lycopodium annotinum L.	f.
Cornus suecica L.	a.	Polypodium Dryopteris L. em Sm.	o.
Solidago Virgaurea L.	f.		
Melampyrum pratense L.	f.	Dicranum scoparium Hedw.	
Trollius europaeus L.	c.f.	Hypnum Schreberi Willd.	
Trientalis europaea L.	o.	Hylocomium splendens B. and S.	
Phyllodoce coerulea Bab.	o.	Lophozia lycopodioides (Wallr.) Cogn	
Geranium silvaticum L.	o.	L. ventricosa Dicks.	
§Aira flexuosa L.	f.		

A still further increase in soil water results in the following "spring flush" type of community:

Salix glauca L.	v.a.—d.	Epilobium alpinum L.	o.
S. nigricans Sm.	o.	Calamagrostis sp.	o.
Betula odorata Bechst.	o.		
§Parnassia palustris L.	o.	Aulacomnium palustre Sch.	
§Geum rivale L.	o.	A. palustre *forma* polycephalum Hubn.	
§Epilobium palustre L.		Dicranum scoparium Hedw.	
var. lapponicum Wg.	o.	Sphagnum Russowii Warnst.	
Eriophorum vaginatum L.	a.	†S. Warnstorfii Rüss.	
Ranunculus acer L.	f.	Hypnum stramineum Dicks.	
Polygonum viviparum L.	f.	†Drepanocladus exannulatus (Gümb.)	
Comarum palustre L.	o.	Warnst.	
Taraxacum sp.	o.	Mnium subglobosum B. and S.	
Geranium sylvaticum L.	o.	Harpanthus Flotovianus Nees.	
Anthoxanthum odoratum L.	o.—f.	Webera sp., perhaps nutans Hedw.	
Rubus chamaemorus L.	o.		

This relatively dense birch community passes over into an open type of wood on the drier, more exposed slopes, and the ground flora loses most of the less

§, † Cf. p. 430.
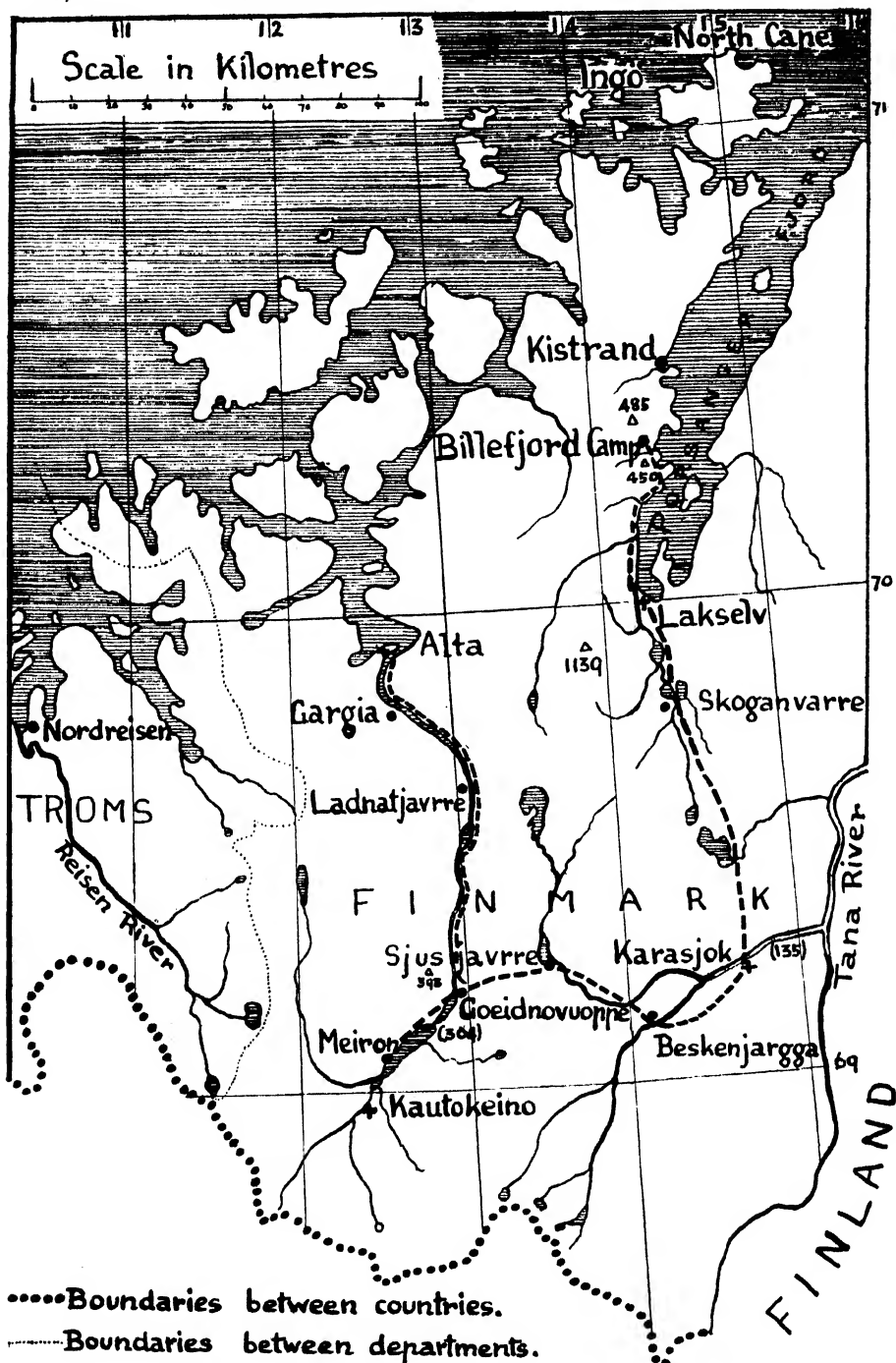
Sketch-map of Finmark. Dotted line joining Billefjord, Meiron and Alta indicates the route
from which observations were made. Altitudes are given in metres.

Phot. 2. Lichen "tundra" area in Billefjordely valley with *Betula nana* and *Salix glauca*.

Phot. 4. Hollow, showing increased length of shoots of *Betula nana* as a result of snow protection. The upper string is stretched along the level top of the *Betula* bush, while the lower is parallel to the surface of the soil (see p. 421).

Phot. W. I.

Phot. 1. View looking east across Billefjordely camp, showing general distribution of vegetation.

Phot. 3. Colonisation of shore of Billefjordely (see p. 419).

LEACH AND POLUNIN—OBSERVATIONS ON THE VEGETATION OF FINMARK

xeromorphic types and usually becomes dominated by *Empetrum nigrum* or *Betula nana*. Here lichens increase in abundance and give a general grey aspect to the vegetation. A further thinning out of the trees to what amounts to an open birch scrub usually occurs along the upward limit of the birch forest: above this again there persists a vegetation composed of the heath types which formed the ground flora of the birch wood lower down. The stunted growth-form so often described as being a characteristic feature of the trees at the upward limit of birch forest in these northern regions was nowhere observed to be very marked.

Thinning out and disappearance of the birches is also often a feature in the lower flat parts of the valleys, where there are wide areas which were obviously lake beds at a not very remote period. From a distance these areas have the appearance of bogs, but close examination reveals the fact that they are for the most part rather dry, on top at least. The Billefjord area of this kind—shown in Pl. XXVI, phot. 2—has a hummocky lichen and *Polytrichum* peat overlying glacial boulders and supporting a sparse phanerogamic vegetation of *Salix glauca* L., *Betula nana* L., *Carex rigida* Good., *Juncus trifidus* L., *Vaccinium uliginosum* L., and *Diapensia lapponica* L. It may well be that a waterlogged, or more probably ice-bound, subsoil accounts for the absence of *Betula odorata*; information on this point, however, could not be obtained. Areas of this kind were the only ones examined which possessed features approaching those of tundra[1].

The shores of the river showed some features of interest. Obviously at no very remote period the stream was much larger than it is at present, and as a result wide stony margins flank its present course in many places. On this stony substratum various successional stages occur, from open detritus with sparse pioneer vegetation to areas covered with damp birch wood similar to that described above.

The following lists show two seral stages which lead up to the birch wood climax (see also Pl. XXVI, phot. 3).

(a) Lowest zone—open community.

Oxyria digyna Hill	a.	*Poa nemoralis L.	o.
*Tussilago Farfara L.	a.	*Anthoxanthum odoratum L.	o.
*Arabis alpina L.	f.	*Phleum alpinum L.	o.
*Astragalus alpinus L.	o.—f.	*Poa alpinum L.	o.
*Cerastium alpinum L. *forma?*	o.	*Luzula campestris D.C.	o.
*Ranunculus acer L.	o.		
Rumex acetosa L.	o.	*Equisetum arvense L.	o.
Taraxacum sp.	o.		
Angelica sylvestris L.	o.	Dichodontium pellucidum Schp.	
*Epilobium alpinum L.	o.	Rhacomitrium canescens	
*Cardamine pratensis L.	o.	var. ericoides B. and S.	
*Pedicularis Sceptrum-Carolinum L.	o.	Bryum pseudo-triquetrum Schwäg.	
*Salix lanata L.	o.	Webera gracilis (Schleich) Lindb.	
*S. bicolor Ehrh.	o.	Philonotis sp.	

* Cf. p. 430.

[1] These areas are similar to those described by Ramann (4) as "Peat Hillock Tundra."

(b) Intermediate zone—closed community dominated by species of Salix.

*Salix nigricans Sm.	a.d.	*Ranunculus acer L.	o.
*S. lanata L.	a.d.	*Hieracium caesium Fr.	o.
*S. bicolor Ehrh.	f.	Taraxacum sp.	o.
Polygonum viviparum L.	f.	*Festuca rubra L. var. arenaria Osb.	f.
*Astragalus alpinus L.	f.	Nardus stricta L.	o.
*Rhodiola rosea L.	o.	*Phleum alpinum L.	o.—f.

The heath zone.

As has already been mentioned, above the limit of the birch forest a heath type of vegetation occurs, excepting, of course, on the exposed summits. This association has a very uniform general appearance and can be seen as far as the eye can reach, covering the rolling plateau region that lies between Porsanger Fjord and the North Sea. The desolate monotony of the landscape is relieved to some extent by the numerous lakes and more or less bare morainic accumulations that lie scattered about in all directions. Over this area the chief dominant species are *Betula nana* and *Empetrum nigrum*. No definite conclusions could be arrived at while examining this area as to the factors that determine the dominance of either one or the other species. As will be seen from the sequel, however, observations made further south in central Finmark suggest that *Empetrum* is markedly more xerophytic than *Betula nana*, so that the average water content of the soil may well be the determining factor.

Below is given a list showing the average floristic composition of this *Empetrum-Betula nana* community compiled from a number of records made in different parts of the area under consideration:

Empetrum nigrum L.	f.—v.a., l.d.	§Calamagrostis lapponica (Wah.)	o.
Betula nana L.	f.—v.a., l.d.	Aira flexuosa L.	l.—l.a.
§Salix glauca L.	l.f.	§Pinguicula vulgaris L.	o.
§S. lapponum L.	l.f.	§Trollius vulgaris L.	o.
§S. lanata L.	l.f.	§Geranium sylvaticum L.	o.
§S. herbacea L.	l.a.	§Bartsia alpina L.	r.
Vaccinium Myrtillus L.	f.—v.a., l.d.		
V. Vitis-idaea L.	o.—f.	Lycopodium alpinum L.	o.—l.f.
V. uliginosum L.	o.—f.	L. selago L.	o.
§Arctostaphylos alpina (L.) Spreng.	l.f.		
§Andromeda polifolia L.	l.f.	Polytrichum urnigerum L.	
§Rubus chamaemorus L.	l.f.	P. juniperinum Willd.	
Cornus suecica L.	o.—f.	Dicranum elongatum Schleich.	
Pedicularis lapponica L.	l.f.	D. fuscescens var. congestum	
Trientalis europaea L.	o.	Husn.	
Phyllodoce coerulea Bab.	o.—l.f.	D. scoparium Hedw.	
Alchemilla alpina L. em Mill.	l.f.	Psilophilum laevigatum (Wah.)	
Solidago Virgaurea L.	o.—l.f.	Lindb.	
Carex rigida Good.	o.—f.	Sphenolobus minutus (Crantz.)	
C. alpicola Wahlenb.	o.—f.	Steph.	
§Scirpus caespitosus L.	l.a.	Lophozia ventricosa	
§Luzula Wahlenbergii Rupr.	o.	var. stemmatina Ach.	
§Juncus trifidus L.	o.	Cladonia coccifera	
§Festuca ovina L.	o.	var. thelephoroides Th. Fr.	
§Anthoxanthum odoratum L.	l.f.		

One conspicuous feature of the area is the presence of frequent and often relatively small hollows that occur, probably owing to the uneven way in

which the glacial accumulations were deposited. The vegetation of these hollows nearly always differs very considerably from that of the type just described as covering the greater part of the plateau as a whole. In such depressions the plants are much taller than on the surrounding area. Even in depressions that are obviously too shallow to provide any appreciable shelter from wind or appreciably to increase soil water-content, the plants present are frequently five to ten times as tall as those outside the hollow. Further, in such slight depressions there is usually a change in the dominant species from *Empetrum* and *Betula nana* to *Vaccinium Myrtillus*. It seems that this effect is due to the protective effect of snow in winter. The snow tends to be largely blown off the level stretches and uniform slopes and to accumulate in the hollows where it affords adequate protection to the taller vegetation. This effect is shown in Pl. XXVI, phot. 4.

A similar influence of snow depth on the tallness of the vegetation is present, though to a less marked degree, on the more uniform hill slopes. As a result we find the vegetation on some slopes to be much taller than that on others. Further, this change in tallness cannot be correlated with any variations in soil, aspect, or exposure. Still another interesting point is the fact that the taller vegetation usually contains a higher percentage of less resistant species such as *Vaccinium Myrtillus*, *Cornus suecica* and *Anthoxanthum odoratum*.

A point worthy of note in connection with *Vaccinium Myrtillus* is that, in the area under consideration, this species appears to be eking out a somewhat precarious existence. Its condition resembles closely that of *Calluna vulgaris* in the English Lake District at altitudes of over 2000 ft. (608 m.), where this latter species attains dominance only in sheltered situations, the characteristic dominant on the exposed hillsides being *Vaccinium Myrtillus*.

Further information regarding factors which determine the general character of the vegetation of this plateau region is yielded by a study of the larger hollows that are frequently to be met with. In addition to showing the snow protection effect just described, these also demonstrate the effect of increased soil water content upon the vegetation. The soil in the bottoms of these hollows is usually much wetter than that of the general hill slopes. It may, in fact, be waterlogged during most of the summer, and in the spring while the snow is melting it may be actually submerged. Such hollows always show two very marked zones of vegetation. On the sloping side occurs a community dominated by *Vaccinium Myrtillus* similar to that already described as filling the shallow depressions. This is obviously a snow protection effect, edaphic conditions being almost identical with those in the surrounding *Betula nana-Empetrum nigrum* community. On the floor of such a hollow, the *Vaccinium Myrtillus* community gives place to a mixed grass-sedge community, the existence of which is obviously due partly to snow protection and partly to increased soil water. Below are given typical lists of the species forming these two zones on the area shown in Pl. XXVII, phot. 5.

(a) *Community on sides of hollow.*		(b) *Community on floor of hollow.*	
Vaccinium Myrtillus L.	v.a., d.	Anthoxanthum odoratum L.	v.a.
Betula nana L. (30–40 cm. tall)	o.	*Phleum alpinum L.	o.
Solidago Virgaurea L.	f.	*Aira flexuosa L.	o.
*Rumex acetosa L.	o.—f.	*Sibbaldia procumbens L.	o.
Trientalis europaea L.	o.	*Rumex acetosa L.	l.a.
Rubus chamaemorus L.	o.	Trientalis europaea L.	o.
*Carex alpicola Wahlenb.	o.	*Betula odorata Bechst. (seedlings)	o.
*Aira flexuosa L.	f.	Pinguicula vulgaris L.	o.
*Athyrium Filix-foemina (L.) Roth.	o.	Solidago Virgaurea L.	o.
		*Carex rigida Good.	f.
		*C. alpicola Wahlenb.	o.

A somewhat different effect of snow, and of the abundance of soil water that is produced by its melting, is shown in those places where snow accumulates and lies until summer is well advanced. Here conditions prevail which are distinctly unfavourable for any but a few hardy or quick growing species. These snow patches give rise to areas of almost bare soil on which occur open communities containing the following species:

*Salix herbacea L.	Dicranella secunda Lindb.
*Ranunculus pygmaeus Wahlenb.	Webera albicans Schp.
*Rumex acetosa L.	Harpanthus Flotowianus Nees.
*Gnaphalium norvegicum Gunn	Calypogeia Trichomanis (L.) Corda.
Oxyria digyna Hill	Lophozia ventricosa Dicks.
Taraxacum sp.	L. Floerkii (Web. and Mohr.) Schiffn.
	L. alpestris (Schleich) Evans
Polytrichum sexangulare Floerke	Moerckia Blytti (Moerck) Brockm.
Pleuroclada albescens (Hook.) Spruce	Cephalozia sp., probably bicuspidata (L.) Dum.
Bartramia ithyphylla Brid.	

A facies of the heath-type vegetation that appears to be chiefly due to edaphic causes is marked by the frequent occurrence of almost pure societies of the fern *Athyrium Filix-foemina* (L.) Roth. These fern societies occur on steep stony slopes in positions similar to those occupied by *Allosorus crispus* Bernh. in England. Associated with the *Athyrium* is nearly always an abundance of *Rumex acetosa*. As is the case with *Allosorus crispus* in England, the presence of *Athyrium Filix-foemina* in Finmark appears to be associated with well-drained soil.

Summit vegetation.

The vegetation of the higher exposed summits is extremely xerophytic in character. It is subjected almost continually both winter and summer to the action of desiccating winds. In the winter, owing to these winds, snow can never accumulate and afford protection to plants. As a consequence we find such summits supporting little plant life other than the lichens which live on the rock surface. Crevices, however, do afford foothold for a few hardy species, and a list of those observed is given below:

Betula nana L.	Arctostaphylos alpina (L.)
Empetrum nigrum L.	Juncus trifidus L.
Vaccinium uliginosum L.	Carex rigida Good.
Dryas octopetala L.	Diapensia alpina L.
Tofieldia palustris Huds.	Pinguicula alpina L.
Pedicularis lapponica L.	Azalea procumbens L.
Phyllodoce coerulea Bab.	Silene acaulis L. *forma*

Phot. 6. Exposed hill-top above Billefjordelv. Showing prostrate *Betula nana* in foreground (see p. 423).

Phot. 8. View looking north across Lakselv (see p. 424).

Phot. 5. Hollow showing zonation described on p. 421. The light-coloured vegetation in the centre is dominated by *Vaccinium Myrtillus*. On the right is the floor of the hollow dominated by grasses.

Phot. 7. Near view of surface of area shown in Phot. 6. Showing prostrate *Betula nana* on right and cushions of *Diapensia lapponica* near lower right-hand corner.

LEACH AND POLUNIN—OBSERVATIONS ON THE VEGETATION OF FINMARK

Pl. XXVII, phots. 6 and 7, show the characteristic appearance of one of these exposed summits. It will be noticed that the ubiquitous *Betula nana* is still in evidence, but here it assumes a prostrate habit with its stems pressed tightly against the surface of the rock, a position which obviously renders it immune from the rigours of the prevailing conditions.

From the foregoing account, it will be seen that the vegetation of the Billefjord region possesses features of considerable interest. The problem of the distribution of *Betula odorata* is one of greater complexity than appears at first sight. The reason why it is confined to the lower altitudes is not at all clear, as apart from the obviously sheltered narrow valleys, and the exposed summit regions, climatic conditions do not appear to vary in any very marked degree over the region. This fact is borne out by the similarity of the ground flora of the more exposed parts of the birch forest to the heath type of vegetation on the plateau. This general similarity between upland and lowland climatic conditions is further suggested in a striking way by a comparison of the type of vegetation described on p. 419 as occurring on the "tundra"-like areas with that occurring on the exposed summits. *Betula odorata* is not protected by snow in its aerial parts, since we learn that in general this only reaches a depth of a few feet in the winter. After consideration of the problem, one is almost inevitably led to the conclusion that the deciding factors relating to the distribution of *B. odorata* are edaphic. As to what these factors actually are, we are not in a position to say definitely, but an investigation of this point would be of considerable value. It seems likely that the winter temperature of the soil may be the limiting factor, and that information regarding the depth to which the soil freezes in winter would provide the clue to the problem.

Some light is thrown on the question by a study of *Betula nana*. This species, as will be seen from what has been said regarding its distribution in the Billefjord region, is able to exist under very varying conditions. One important reason for this appears to be the ease with which it is able to adjust its shoot system to suit the particular situation in which it is growing. We consequently find it varying from large bushes, 1 metre or more in height when growing in sheltered positions, to the close-growing prostrate form of the exposed summits. The roots of *B. nana* can certainly survive freezing in the winter. With its roots in a frozen condition, its existence obviously depends upon its successfully providing against desiccation by means of the adaptability of its shoot system. On the other hand, in *B. odorata* we. have a tree which does not possess similar adaptability of its shoot system, and consequently it may be that the winter evaporation from the leafless branches brings about desiccation and death if the roots are in frozen soil and are consequently unable to absorb water. The roots of this species penetrate deeper into the soil than those of *B. nana*, and it may be that the greater amount of snow in the valley regions prevents the soil from freezing to as great a depth as it does in the upland regions with their thinner layer of snow.

Lakselv Region.

The general nature of the Lakselv district and its vegetation is clearly shown in Pls. XXVII and XXVIII, phots. 8 and 9. The greater part of this area is covered with dry *B. odorata* forest, developed on river deposits of pure sand. On the eastern side of the Lakselv river the ground rises in a series of well-marked steps formed by river terraces, while on the western side the river flats terminate abruptly in an almost perpendicular cliff about 1000 ft. (304 m.) in height, against the face of which are extensive talus accumulations. The forest in this region shows unmistakable evidence of having been modified by human interference. Between Lakselv village and the head of the Porsanger Fjord, there is a considerable admixture of somewhat stunted pines (*Pinus sylvestris*) with the abundant birches. There are also many pine stumps that have sprouted out from their bases and produced prostrate branches, all of which were found to be bearing cones. There appears to be ample evidence that here the natural forest was originally pine forest, but the cutting of trees for firewood, etc., has resulted in a change to birch forest.

Considerable stretches of the forest area surrounding the scattered Lapp huts have been completely cleared of trees and are covered by a poor dry type of pasture.

Below is a composite list (species determined by Mr Wilmott) from various pastured areas in the Lakselv district—almost always river-deposited sand:

Empetrum	l.d.	Antennaria dioica (L.) Gaertn.	
Vaccinium uliginosum L.	f.—a.	Rumex acetosella L.	
V. Vitis-idaea L.	f.—a.	Poa caesia S.	
Festuca rubra L.	a.—l.d.	Pedicularis lapponica L.	
F. ovina L.	f.	Linnaea borealis L.	
Campanula rotundifolia L.	o.—f.	Sagina nodosa (L.) Fenzl.	
Achillea Millefolium L.	o.—f.	Gentiana nivalis L.	
Calamagrostis neglecta Ehrh.	f.	Dryas octopetala L.	
Poa pratensis L.	f.	Taraxacum officinale (Web.) Wigg.	
Stellaria media (L.) Cyr.	l.a. near huts	Astragalus alpinus L.	
Poa annua L.	l.a. near huts	Salix phylicifolia L.	
Equisetum arvense L.	l.f.	S. nigricans × phylicifolia	
Polygonum viviparum L.	o.	Betula odorata Bechst.	
Solidago Virgaurea L.	o.	Eriophorum sp. or spp.	
Ranunculus acris L.	o.	Parnassia palustris L.	
Allium sibricum L.	o.	Rumex acetosa L.	
Silene acaulis L.	o.	Saussurea alpina (L.) DC.	

The occasional plots fenced off for hay have grasses completely dominant and sometimes forming good turf. The following list (Mr Wilmott's determinations) was taken from such a dry fenced-in hay plot:

Festuca rubra L.	a.—d.	Matricaria inodora L.	o.
F. ovina L.	f.	Pedicularis lapponica L.	o.
Poa caesia Sm.	l.f.	Campanula rotundifolia L.	o.
Polygonum viviparum L.	o.—l.a.	Equisetum pratense L.	o. in damper parts
Achillea Millifolium L.	o.	Ranunculus acris L.	o.

The only crops of these regions are potatoes and oats, both grown in small plots. The oats will not ripen and are cut for fodder; in and around these

cultivated plots, as well as by the walls of the Lapp huts, grow the following weeds (determined by Mr Wilmott), mostly typical of an open soil surface:

Chenopodium album L.	Stellaria media (L.) Cyr.
Poa annua L.	Matricaria inodora L.
Draba incana L. *forma* hebecarpa	Cerastium glabratum Hartm.
Rumex acetosella L.	Urtica dioica L.
Capsella Bursa-pastoris (L.) Med.	Sinapis arvensis L. growing only in the oats
Polygonum aviculare L.	

The birch forest is of a decidedly more xerophytic type than that in the Billefjord region owing to the extremely porous nature of the soil; the following is a typical list of species present:

Betula odorata Bechst.	d.	Azalea procumbens L.	o.
Pinus sylvestris L.	o.	Pedicularis lapponica L.	o.
Juniperus communis L.	o.	Solidago Virgaurea L.	r.
Vaccinium Vitis-idaea L.	a.—v.a.	Juncus trifidus L.	r.
V. myrtillus L.	o.	Polygonum viviparum	r.
V. uliginosum L.	o.—f.	Linnaea borealis L.	o.
Empetrum nigrum L.	a.	Pyrola secunda L.	o.
Festuca ovina L.	o.—f.	Trientalis europaea L.	o.
Aira flexuosa L.	f.—a.	Lycopodium annotinum L.	o.

Scree vegetation.

The vegetation of the screes at the foot of the cliffs along the western bank of the river present features of interest in relation to a previously published account of this type of plant community by one of the present writers (1).

These Lakselv screes, when examined from a point at some distance from them where a general view can be obtained, present an appearance very similar to that of the screes of the English Lake District (1). Colonising vegetation occurs and forms the usual system of vertical strips. Closer examination reveals the fact that most of these strips consist almost entirely of birch and rowan trees, apparently growing on the active parts of the scree. At intervals along the talus accumulation, however, there are to be found patches of varying size which show a more or less complete covering of vegetation with consequent stabilisation of the scree surface. The dominant species on these fully developed stabilised areas is *Betula odorata* (trees up to 4 m. tall), with *Sorbus Aucuparia* (trees 1–3 m. tall), as a frequent associate. A well-developed ground flora is present beneath the trees, as is indicated by the following list which gives the composition of a typical fully developed community occurring on a stable area of the scree.

*Betula odorata Bechst.	d.	Epilobium angustifolium L. em Curt.	f.—l.a.
Sorbus Aucuparia L.	f.	Linnaea borealis L.	o.
Populus tremula L.	o.	*Rumex acetosa L.	o.
Betula nana L.	o.	Campanula rotundifolia L.	o.
Vaccinium Myrtillus L.	a.	Antennaria dioica Gaert.	l.f.
V. uliginosum L.	a.	Empetrum nigrum L.	l.a.
V. Vitis-idaea L.	a.	Polypodium Dryopteris L.	l.f.
Solidago Virgaurea L.	o.	*Athyrium Filix-foemina (L.) Roth.	o.
*Aira flexuosa L.	f.		

The species involved in the initial stages of the colonisation of the scree, leading up to the formation of one of these relatively stable patches of vegetation, appear to be chiefly rhizomatous forms, viz. *Vaccinium Myrtillus,*

V. uliginosum and *V. Vitis-idaea.* No indications were observed of the bryophyte-fern succession which frequently appears on British screes (1). Apparently the rhizomatous species spread over the stretches of scree that have, after a general mass movement of fragments, assumed an angle of comparative stability. The stabilising and soil-forming reaction of these plants allows of the development of various seedlings including those of the already mentioned trees. Meanwhile, rock fragments continue to fall from the weathering crags above the vegetation area, but the presence of the patch of vegetation may for a long time prevent them from sliding downwards. This continued accumulation of fragments, however, results in the piling up, at an unstable angle, of a huge mass of talus above the stabilised area. Eventually the weight of this mass becomes too great for the stabilising forces and it slides downwards, carrying with it, and destroying or burying, the colonising plants. After such a movement has occurred, all that remains to be seen of the original patch of vegetation are the tops of the larger trees, whose trunks and roots have withstood the shock to a greater or less degree. These trees continue to grow, surrounded by bare active scree, and form the conspicuous green vertical strips (see Pl. XXVIII, phots. 10–12).

It is obvious that the characteristic features of these Lakselv screes are largely due to climate. The extreme conditions of alternating heat and cold during the summer result in a rapid weathering of the crags and consequent rapid accumulation of fragments. Also the alternate melting and freezing of snow in the spring must be an important factor in the initiation of the general mass movements of the talus, which result in the destruction and burial of the vegetation-covered areas as described. Conditions on these screes appear to be very similar in many respects to those described by Hess for some Swiss screes (2). On the other hand, when we compare the Lakselv screes with those occurring in the British Isles, we find marked ecological differences between them which can be correlated with differences in the existing climatic conditions.

CENTRAL FINMARK.

South from Lakselv the dry birch woods, with greater or less admixture of pines, described in the last section, form an almost unvarying community as far as Skoganvarre. As the distance from the Porsanger Fjord increases, the pines become taller, and in places more numerous, until round Skoganvarre patches of pure high forest of pine occur.

As we journeyed south and left the Lakselv valley, we passed out of the pine zone and entered the zone of natural birch forest. Here conditions appear to be less xerophytic than round Lakselv, and consequently a more luxuriant ground flora occurs beneath the trees. The composition of this forest closely resembles that described on p. 417, as occurring in the Billefjordelv region, except that *Vaccinium Myrtillus* appears to be more abundant, often being the dominant constituent of the ground flora. In the low-lying regions bordering the lakes, the birch forest gives place to dwarf-willow communities

Phot. 10. Colonised area on scree near Lakselv (see p. 426).

Phots. W. L.

Phot. 12. Surviving *Betula odorata* in active scree after destruction of colonised area similar to that shown in Phot. 10.

Phot. 9. View taken from river terrace near Lakselv, looking up the river towards the south-west.

Phot. 11. Accumulation of talus above area shown in Phot. 10. Note *Epilobium angustifolium* in centre.

LEACH and POLUNIN—Observations on the Vegetation of Finmark

and to areas covered with *Polytrichum*—peat on which grows abundance of *Betula nana* and *Rubus chamaemorus*. On the high ground the forest thins out and the usual *Betula nana-Empetrum nigrum* communities occur.

As the Karasjokka river valley is reached the zone of *Pinus sylvestris* is again entered. This species forms high forest on either side of the river at Karasjok, while round the town cutting has in many places resulted in a considerable admixture of *Betula odorata*, but not to the same disastrous extent as round Lakselv. The pines, however, appear to be almost entirely confined to the river valley slopes; immediately these are left, birch again becomes dominant. This is very noticeable along the route from Karasjok to Beskenjargga; leaving the river valley one returns to the birch forest and upland heath communities until the river is again approached further west. Immediately the ground begins to slope down again to the river the pines begin to reappear, becoming more and more numerous as the river is approached.

It would seem that the pines owe their existence in this region to the shelter afforded by the valleys, since, at an altitude of about 1000 ft. (304 m.), they disappear and there occurs *Betula odorata* forest frequently with a shrub layer of *Betula nana*, about 2 ft. (61 cm.) high, the ground flora being an *Empetrum nigrum-Vaccinium Myrtillus-V. uliginosum-V. Vitis-idaea* community. Near this upward limit of *Pinus sylvestris*, the pines frequently lose their pyramidal form owing to the dying off of their topmost branches, an unmistakable sign that they are nearing the point where climatic factors are becoming too severe for them. Bryophytes and lichens collected from the birch-pine forest round Beskenjargga are given in the following list:

Polytrichum strictum Banks
P. commune L.
Hypnum Schreberi Willd.
Dicranum fuscescens var. congestum Husn.
Sphenolobus minutus (Crantz.) Steph.
Ptilidium ciliare (L.) Hampe.
Lophozia Binsteadii (Kaal.)
L. Kunzeana (Hub.) Evans
L. Hatcheri (Evans) Steph.

L. lycopodioides (Wallr.) Cogn.
Cladonia gracilis (L.) Willd.
C. uncialis (L.) Web.
C. crispata (Ach.) Flot.
C. deformis Hoffm.
C. rangiferina (L.) Web.
Nephroma arcticum (L.) Fries
Peltigera aphthosa (P.) Willd

Leaving Beskenjargga we travelled in a west-south-westerly direction from the Karasjokka river to Meiron on the Kautokeino river, the distance between these two places as measured along a straight line on the map being about 80 km. This tract of country[1] between the two rivers is undulating in character and is intersected by numerous small streams, along the courses of which are numerous lakes both large and small. From about 15 km. west of Beskenjargga to beyond the Kautokeino river, the soil is composed almost entirely of a thick deposit of sand with numerous scattered boulders, obviously laid down under water during the retreat of the ice at the end of the last period of glaciation. In many places the surface is scooped out into deep valleys and hollows, now quite dry, but unmistakably due to the action of swift currents.

---

[1] The vegetation of this area apparently closely resembles that of the adjoining area of Swedish Lapland as described by Simmons (5).

Over the whole of this area the most frequent consociation is a dry open birch forest (see Pl. XXIX, phot. 13). This forest shows the usual local variations in relation to increased soil water in the stream valleys and round the lakes, and the usual change to the heath association on the hills above the tree limit; no important change being observed from what has already been recorded regarding the species present (see Pl. XXIX, phot. 14). On the whole, however, this inland region shows evidence of being much drier than the more northerly regions dealt with in the previous section of this paper. Over the greater part of the area conditions are too dry to support a continuous closed phanerogamic vegetation. A great part of the soil is clothed only with xerophytic mosses and lichens and of the latter, the reindeer moss, *Cladonia rangiferina* (L.) Web., is the most abundant and most conspicuous, giving a whitish aspect to the whole landscape. In many places the sand is quite bare except for *Polytrichum juniperinum* (Willd.) and *P. piliferum* Schreb., which are almost as universally important in the rôle of sand binders as they frequently are in the British Isles (3). In this dry *Betula odorata* zone the relation of the vegetation to the combined edaphic and climatic factors is very marked. Owing to its sandy nature the soil has a very low water-retaining capacity, and the effect of this on the vegetation is emphasised by the high evaporation rate due to a dry atmosphere and almost continuous insolation during the summer months. The result of this combination of factors is that the ground flora beneath the birches on north-facing slopes differs in a marked degree from that developed on level ground and on south-facing slopes. In the case of the former even where the slope is only slight the obliquity of the sun's rays owing to its low altitude results in an evaporation rate near the surface of the soil which is low enough to permit of the development almost everywhere of a more or less complete covering of phanerogamic species. Such a slope is shown in Pl. XXIX, phot. 15, and the composition of the community forming the ground flora was found to be as follows:

Empetrum nigrum L.	v.a.—d.	Hypnum Schreberi Willd.
Arctostaphylos uva-ursi Spr.	l.d.	Polytrichum juniperinum (Willd.)
Vaccinium Vitis-idaea L.	f.—a.	P. piliferum Schreb.
V. Myrtillus L.	o.—f.	P. strictum Banks
V. uliginosum L.	o.—f.	Lophozia Hatcheri (Evans) Steph.
*Aira flexuosa L.	o.	L. ventricosa Dicks.
*Calamagrostis lapponica (Wahl.) Hartm.	o.—f	Stereocaulon paschale (L.) Fr.
		Cladonia cornuta (L.) Schaer.
Juniperus nana L.	o.	C. rangiferina (L.) Web.
Solidago Virgaurea L.	o.	C. cenotea (Ach.) Schaer.
		C. to subgenus Cladina, probably
*Lycopodium annotinum L.	o.	alpestris (L.)
		C. alpicola (Flot.) Vain.
Dicranum elongatum Schleich.		C. deformis Hoffm.
D. fuscescens var. congestum Husn.		Cetraria cucullata Ach.

On the other hand, on the level and on the south-facing slopes the sun's rays strike the ground at a less oblique angle. The result is that the rate of evaporation is higher, and except in the shade cast by the birch trees, reaches an intensity which inhibits the growth of phanerogams. The effect of this is

Phot. 14. View looking S.E. from above tree limit near Anjovarre. Open Betula nana-Empetrum nigrum-lichen community in foreground. Lakes and B odorata forest in distance (see p. 428).

Phot. 16. Open Betula odorata forest on level ground near Goeidnovoppe. Note restriction of phanerogams to regions sheltered by birch trees (see p. 429). Photos. W. L.

Phot. 13. Dry open Betula odorata forest near Goeidnovoppe (see p. 428).

Phot. 15. North-facing slope near Goeidnovoppe showing development of phanerogamic ground flora (see p. 428).

LEACH AND POLUNIN—OBSERVATIONS ON THE VEGETATION OF FINMARK

shown in Pl. XXIX, phot. 16, in which it will be seen that in the shade of each tree there is a well-developed community of a similar composition to that which covers the whole area on the north-facing slopes (see list above). The intervening areas between these shade patches are covered with the lichens and xerophytic mosses also given in the list.

The birch trees on these dry areas grow to a height of 4–5 m., and their trunks average about 12 cm. in diameter. The open spacing of the trees, which are 4–5 m. apart, is obviously a root competition effect, the available soil water being in their case also the limiting factor.

The immediate effect of increased soil water on the birch forest is well marked here as elsewhere. On the lower lying regions near the rivers and lakes, the trees grow much taller and form a close canopy with a luxuriant ground flora. A typical composition of such a community at the side of the Kauto-keino river at Goeidnovoppe is as follows:

Betula odorata Bechst.	d.	Dicranum elongatum Schleich.	
B. nana L.	l.f.	D. fuscescens var. congestum Husn.	
Vaccinium Myrtillus L.	a.—v.a.	Polytrichum commune L.	
V. uliginosum L.	f.—a.	Lophozia Floerkii (Web. and Mohr.)	
V. Vitis-idaea L.	f.	Schiffn.	
Empetrum nigrum L.	a —v.a.	L. Kunzeana (Hub.) Evans	
Rubus arcticus L.	f.	L. ventricosa Dicks.	
Pyrola secunda L.	o.	Sphenolobus minutus (Crants.) Steph.	
Cornus suecica F.	o.	Stereocaulon paschale (L.) Fr.	
Solidago Virgaurea L.	l.f.	Cladonia bellidiflora (Ach.) Schaer.	
Aira flexuosa L.	f.	C. fimbriata (L.) Fr. var. simplex Weis.	
Epilobium angustifolium L.	o.	C. alpestris (L.) Rabenh.	
		C. crispata (Ach.) Flot.	
Lycopodium alpinum L.	l.f.	C. uncialis (L.) Web.	
*L. annotinium L.	f.	C. coccifera var. pleurota (Flk.) Scaer.	
Equisetum sylvaticum L.	f.	Nephroma arcticum (L.) Forss.	

In the low-lying areas bordering the rivers there frequently occur depressions that recently must have been occupied by shallow lakes. On such sites a typical acid bog peat has developed on which grow such species as:

Betula nana L.	a.—v.a., l.d.	Hypnum Schreberi Willd.	
Rubus chamaemorus L.	a.—v.a., l.d.	Dicranum Bergeri Bland.	
Andromeda polifolia L.	o.—f.	Lophozia attenuata (Mart.) Dun.	
Empetrum nigrum L.	f.—a.	L. Binsteadii (Kaal.)	
Vaccinium Myrtillus L.	f.	Calypogeia Tricomanis (L.) Corda	
V. uliginosum L.	f.	Aneura latifrons Lindb.	
Eriophorum vaginatum L.	f.	Cephalozia sp.	
		Cladonia gracilis (L.) Willd.	
Sphagnum fuscum (Schimp.) Klingg.		C. cornuta (L.) Schaer.	
Leptoscyphus anomalus (Hook.) Mitt.		C. cornuta (Ach.) var. cressota Ach.	

A further list which may be of some ecological interest is given below; it includes the bryophytes collected from the boulders and clay along the eastern shore of the Kautokeino river at Goeidnovoppe.

Hypnum Patientiae Lindb.	Rhacomitrium canescens Brid.
H. Schreberi Willd.	Bryum pseudo-triquetrum Schaeg.
H. cupressiforme	Lophozia Kunzeana (Hub.) Evans
Aulacomnium palustre Schwaeg.	L. ventricosa Dicks.
Polytrichum urnigerum L.	L. quinquedentata Huds.
Fissidens osmundoides Hedw.	Scapania irrigua (Nees.) Dum.
Trichostomum tortuosum Dixon	Alicularia scalaris (Scrad.) Corda
Cynodontium Wahlenbergii Ren. and Card.	Preissia quadratus (Scop.) Nees.
Drepanocladus uncinatus	

This dry birch community, so far as observations were possible, was found to extend from Meiron down the Kautokeino river beyond Ladnatjavrre. Near the mouth of the river, up to and beyond Gargia, pine forest occurs which is very similar to that at Karasjok.

Specimens of the plants mentioned in this account were in most cases brought back for identification. All the bryophytes and lichens with the exception of those marked (†) were named by Carl Stenholm of Göteborg, Sweden. Those marked (†) were named by W. R. Sherrin.

Of the vascular plants, those marked (*) were named at the Herbarium of the Royal Botanic Gardens, Kew (the vascular cryptogams and grasses by Mr F. Ballard, *Hieracium caesium* Fr. by Mr A. R. Horwood, and the remainder by Dr W. B. Turrill), while those marked (§) and the lists specially indicated were named by Mr A. J. Wilmott of the British Museum. To all these gentlemen the cordial thanks of the authors are due. The senior author accepts responsibility for the naming of the unmarked vascular plants[1].

Thanks are due to the University of Oxford, under whose auspices the expedition was organised by the O.U. Exploration Club, for a grant towards the expenses of the expedition and to the Joint Standing Committee for Research of the University of Birmingham for a similar grant: also to Christ Church and Magdalen College, Oxford, which likewise made contributions towards expenses.

REFERENCES.

(1) Leach, W. "A preliminary account of the vegetation of some non-calcareous British screes (Gerölle)." This JOURN. **18**, 1930.

(2) Hess, E. "Über die Wuchsformen der alpinen Geröllpflanzen." *Beihefte z. Bot. Cent.* **27**, 1911.

(3) Leach, W. "On the importance of some mosses as pioneers on unstable soils." This JOURN. **20**, 1931.

(4) Ramann, E. *The Evolution and Classification of Soils.* Cambridge, 1928.

(5) Simmons, H. G. "Die Flora und Vegetation von Kiruna im schwedischen Lappland." Engler's *Bot. Jahrb.* **48**, 1912.

[1] The nomenclature and species standard followed is that of Blytt, *Haandbogi i Norges Flora*, Kristiania, 1906.

REVIEWS

Naumann, E. *Die Binnengewässer*. Band xi: Grundzüge der regionalen Limnologie. Schweizerbartsche Verlagsbuchhandlung, Stuttgart, 1932. Pp. xiv + 176. Price 19 marks, unbound.

Regional limnology aims at a classification of fresh waters on a regional basis and, according to Naumann's view, should be based primarily on their productivity. Causal investigation is thus directed, in the first place, to a study of the factors conditioning the development of holophytic vegetation. These are grouped by Naumann under the main headings: temperature, light, content of nutritive material, quantity of detritus (clay or organic), and gas content. For each of these he distinguishes three intensities—the polytrophic, mesotrophic, and oligotrophic grades—according as the factor in question is of a high, medium or low grade. In this way, for each piece of water he establishes an ecological spectrum, characterised by the trophic grades of the various factors.

Among the nutritive factors those of maximum importance are found in the calcium, nitrate and phosphate, iron and humus spectra. Polytrophy of the calcium factor is characteristic of alkalitrophic, oligotrophy of the nitrate and phosphate factor of oligotrophic, and polytrophy of the factor of eutrophic waters. Polytrophy of the humus-factor distinguishes dystrophic and of the iron-factor siderotrophic waters. Waters with an extreme (low) pH are acidotrophic, while those with abundant clay detritus (clay polytrophic) are described as argillotrophic.

After considering diverse other methods of grouping, waters are broadly classed into two series, eutrophic and oligotrophic with respect to their content of available nitrates and phosphates. The eutrophic type is characterised by its abundant phyte 'ankton which usually gives a definite coloration to the water, often with the production of water flowers; such eutrophy is commonly combined with argillotrophy or with slight dystrophy. The oligotrophic type is distinguished by a scanty phytoplankton, which is never sufficient to lend a colour to the water, but the deficiency of mineral salts conditioning this may be due to many different causes, so that Naumann distinguishes the following sub-types of the oligotrophic series: the harmonious oligotrophic, the extreme alkalitrophic, the dystrophic, the argillotrophic, the acidotrophic, and the siderotrophic. Actual deficiency of nitrates and phosphates does not occur in all these sub-types, but, owing to the polytrophic development of some other factor, they are not present in an available form (e.g. alkalitrophic or siderotrophic waters).

In a subsequent section Naumann deals with the regional distribution of the factors affecting productivity, which are specially illustrated for South Sweden, for which alone comprehensive data are available. This is followed by a consideration of alpine lake-types in relation to productivity on the basis of the work of Gams, Haempel, and Pesta, those of arid regions mainly on the lines of Decksbach's investigations, and those of the humid tropics in accordance with the recent work of Ruttner and Thienemann. The regional distribution of dominant organisms and communities in relation to the determining factors is illustrated by reference to selected examples, present knowledge not admitting of a wider treatment. Other sections deal separately with plankton, littoral, and profundal communities from the regional point of view. The general conclusion reached by the author is that the basis of regional limnology must be sought in the interpretation of the diverse types of waters as an expression of the productive capacity of the environment and that from this point of view attention must be focused on the plant-physiological aspects of the problem.

Final sections of the book deal with succession and economic aspects. There can be no doubt that Naumann's work is stimulating in its outlook and that its ultimate aim is one well worthy of achievement. The numerous problems and the present position are clearly put, but the author's method of dividing the subject-matter into numerous sections, many of them exceedingly brief, scarcely makes for easy reading, and one cannot help feeling that there is much repetition which leads to a longer treatment than the present position of the subject warrants. The subject-matter is illustrated by a number of excellent photographs and there is a comprehensive list of literature with 350 references.

F. E. FRITSCH

The Journal of Animal Ecology. Vol. I, No. 1, May 1932. 100 pp. Cambridge University Press. Price: Single Numbers 22s. 6d., Annual Subscription 30s. (25s. to members.)

The contents of the first number cover varied groups of animals, studied in relation to modern ecological ideas: gall-flies on wheat and their insect parasites (H. F. Barnes), asilid flies and their varied insect prey (B. M. Hobby), wood ants and their aphid farms and bird enemies (C. Elton), birds on Oxfordshire farmland (W. B. Alexander), rooks in Cheshire (B. J. Marples), birds in Brazil (J. T. Cunningham and D. M. Reid), fruit-bats in the Australian forests (F. Ratcliffe), diseases of fox 3 (G. Tickner) and rabbits (A. D. Middleton) in England, and seals on the Scottish islands (T. H. Harrisson). The limitation mainly to terrestrial animals will be corrected in future issues, which will contain work on freshwater and marine groups as well. Problems of population rank first: the grouping of ants and of rooks into territories, with the allied problem of movements between different habitats for feeding, breeding or roosting (illustrated by the Brazilian birds, English rooks and Australian fruit-bats); densities of numbers of birds and seals and insects (expressed by Alexander for birds in weights per acre); seasonal trends in the density of birds; fluctuations from year to year in gall-flies, ants and other forms; causes of mortality; and migration in relation to food and other factors, seen most impressively in the occasional invasions and in the daily flights of fruit-bats. Ratcliffe's paper contains good photographs of some of the typical forest types of Australia. Many of the papers contain quantitative records which will form the basis for future comparisons and analyses. There are thirty-nine short notices of British papers on animal ecology, and three reviews. The papers contained in this first number and those already received for future issues confirm the idea that there is a growing mass of British work on animal ecology which has a common fund of ideas, although related to very diverse groups of animals, and is approaching exact quantitative expression (though this is not yet always achieved). The launching of a new journal which, on the animal side, can consolidate and expand the policy initiated and fostered by the *Journal of Ecology* is thus fully justified.

CHARLES ELTON

Supplement IX

BRITISH EMPIRE VEGETATION ABSTRACTS:

TITLES AND ABSTRACTS OF PUBLICATIONS ON THE VEGETATION AND ECOLOGY OF THE OVERSEAS EMPIRE AND ON RELATED TOPICS

(1) CANADA (COLLABORATOR, J. E. DANDY)

549. Bird, R. D. "Biotic Communities of the Aspen Parkland of Central Canada." *Ecology*, **11**, pp. 356–442, Figs. 1–15, Plates 12–18. 1930. (1. 146.)

The Great Plains region of central North America is separated from the deciduous forest on the east and the coniferous forest on the north by a narrow belt of country, in which forest and prairie intermingle. This is characterised by forest extending far into the prairie along the rivers, and groves of trees interspaced by prairie which is found to be gradually crowded out as the forest is approached. Such country is called by some biologists savanna, but more generally parkland.

Two types of parkland may be recognised in central North America, one (characterised by oak and hickory groves) between the eastern deciduous forest and the true prairie, the other (characterised by aspen groves) between the northern coniferous forest and the true prairie. Each represents an ecotone or area of stress between forest and grassland formations, and may generally be considered as a sub-climax community or associes of the former. In extensive areas, however, the dominant trees of the forested parts of the parkland may form a false climax community or separate association of the forest formation. This is possibly the condition of the aspen over the greater part of the aspen parkland.

The aspen parkland, except for small areas in northern North Dakota and north-western Minnesota, is confined to Canada. It extends from a short distance south of the Manitoba-Minnesota boundary north-westwards in a line varying in width from 50 to 150 miles to a point near Edmonton, Alberta, and from there southwards in a narrow strip some 25 miles in width along the foothills of the Rocky Mountains to the Old Man River. In addition, it is found in isolated areas in the Turtle Mountains in Manitoba; in the Moose Mountains, Wood Mountains, Cypress Hills, and Great Sand Hills in Saskatchewan; and in several small areas along the tributaries of the Peace River in Alberta. Throughout this region the dominant tree of the woodland is the aspen, *Populus tremuloides*. In places there are fair stands of other trees, Manitoba maple or box elder (*Acer negundo*), elm (*Ulmus americana*), bur oak (*Quercus macrocarpa*), and balsam poplar (*P. balsamifera*); but in all cases the succession is towards aspen. The forests of the region may be considered as consisting of an aspen association and of associes of the other trees mentioned. On the north the aspen is in some places being replaced by white spruce (*Picea canadensis*). This replacement is slow, and, in the opinion of the author, largely controlled by edaphic conditions, for the spruce seems to be very partial to rocky and sandy soils. It is found to the south in soils of this nature, e.g. in the sandhills near Carberry, Manitoba, indicating that spruce was scattered over the whole area and that the trees have died or that they never gained a foothold in the intervening land. These isolated areas may be explained by spruce following close behind the ice as it receded at the end of the glacial period and remaining wherever conditions are favourable.

The aspen parkland thus forms an ecotone between the prairie and the coniferous forest. It is replacing the prairie over practically all its southern front, and to the north in some localities at least is in turn being replaced by spruce.

For his study of the parkland region the author selected stations for intensive study and made headquarters at Birtle, Manitoba, within 15 miles of the Saskatchewan boundary. This region was particularly favourable, as it is in the heart of the parkland and presents many seral stages in a state as yet relatively undisturbed. In addition, trips were made to other points for the purpose of comparison and the study of succession. Districts about Winnipeg, Treesbank, Molson, and Mafeking in Manitoba and about Saskatoon and Quill Lake in Saskatchewan were visited.

The major biotic communities (including plants and animals) of the aspen parkland are described in detail by the author under the divisions: (A) Prairie Community; (B) Willow Communities, (1) *Salix petiolaris* Consocies and (2) *Salix longifolia* Consocies; (C) Aspen Communities, (1) Aspen Edge Community and (2) Mature Aspen Forest Community. A section on coaction, seasonal phenomena, and biotic succession in the aspen parkland is followed by a discussion, summary, bibliography, and appendix.

550. Raup, H. M. "The Distribution and Affinities of the Vegetation of the Athabasca-Great Slave Lake Region." *Rhodora*, **32**, pp. 187–208, Figs. 1–37. 1930. (1. 147.)

A study of the flora of the Athabasca-Great Slave Lake region, in north-western Canada, has revealed certain outstanding features of distribution and affinity. In the present paper the author, who with his wife was engaged for four summers in botanical survey operations in the region, takes the opportunity to make a brief statement of the major problems involved.

A section of the vegetation reaching from the Slave River westwards to Moose Lake, about 75 miles away, shows a variety of types, ranging from the flood plain sloughs of the lowlands to the prairies and thick timber on the higher ground. Examination of the distribution of these types soon suggests a strong correlation with the topographical features of the region, and leads to an investigation of the geological and physiographical processes which have produced this topography. Botanising and comparing notes and collections with similar situations in other regions, one is impressed with the openness of the plant associations and with the comparatively small number of species involved in them. The plants that are there show affinities with floras of widely separated regions, while many of the common species of the Canadian forests elsewhere are absent or very rare in the Athabasca-Great Slave Lake district.

The principal subjects discussed by Raup in this paper are the topographical history of the Athabasca-Great Slave Lake region, the distribution of the vegetation, the affinities of the flora, and the absence from the region of certain Canadian forest plants. His illustrations include maps showing the geographical ranges of 29 species and varieties, and in addition he gives a table showing the distribution of Canadian forest plants.

551. Raup, H. M. "The Vegetation of the Fort Reliance Sand-plain." *Ann. Carnegie Mus.* **20**, pp. 9–38, Figs. 1–2, Plates 1–6. 1930. (1. 148.)

The Fort Reliance sand-plains are situated at the eastern extremity of Great Slave Lake, Mackenzie. A survey of their vegetation was carried out in August 1927, and the results are presented in this paper. According to the author's summary, ancient lake bottoms, glacial moraines, and extinct shore lines show that in post-Glacial time there was a series of "Hyper-Great Slave Lakes" in the basin of the present lake. At the withdrawal of the ice there

was probably a differential isostatic readjustment of the surface of the land and a lowering of lake levels due to the opening of drainage channels, so that these ancient beaches and lake bottoms now lie at varying heights above the present level. Those at the eastern end of the Great Slave Lake basin are the highest ones, those at Fort Reliance being 600 ft. above the present lake.

The Lockhart River, in its lower course and at its entrance into the lake, has cut its way through the ancient beaches which are there composed of sand. The Fort Reliance area is at the mouth of this river, where the sand is being eroded away and redeposited by the river and by the waves of the lake. A series of sand terraces is being formed in one place, and a series of prograding beaches in another. This process is bringing into existence new ground upon which vegetation may grow. Since it is evident from the configuration of the shore and the topography that the local land forms have come into existence in very much the same manner as new land is doing now, then, if the development of the vegetation on the new areas can be outlined, that on the older areas can be outlined also.

Four types of new habitats are being formed: (1) the prograding beach; (2) the beach lagoon; (3) the margin of the traversing stream; (4) the sliding sand of the erosion terrace. The first of these is the only important one in the production of the park-like vegetation of *Picea canadensis* and *Betula alaskana*, with its ground cover of *Cladonia* and *Cetraria*. The successions involved take place upon the ridges and the inter-ridge areas of the prograding beach. The plant associations of the beach lagoon and stream margins start as hydrophytic successions, but become xerophytic, like that of the prograding beach, after the emergence of the land has lowered the water table in the soil. The vegetation of the sliding bank is ephemeral, and has little significance, except for its retarding effect on the movement of the sand. A fifth type of succession is not represented at present, but probably may occur during periods of more or less rapid uplift, when the terrace now building off shore is raised. A more or less level plain would then be exposed, and a plant association would develop in a succession probably not materially differing from that of the present prograding beach.

The xerophytic nature of the more recent sand plains seems to have been altered on those which are older and higher by the accumulation of humus and by the increased capacity of the soil to hold water. The arboreal growth becomes denser, and a distinct layer of muskeg shrubs appears.

There is no evidence of fire in the timber during the past 63 years. Biotic influences, including those of man, do not seem to have been of great importance in governing the present nature of the vegetation.

The rate and manner of the changes, both physiographical and vegetational, have probably been much altered in post-Glacial time due to climatic changes. A progressively longer open season since the recession of the glacier may gradually increase the rate of change.

552. Brand, A. "Die Amerikanischen Arten der Gattung *Lithospermum*." *Fedde, Repert. Sp. Nov.* **28**, pp. 10–17. 1930. (1. 149.)

In this paper Brand gives a conspectus of the indigenous American species of *Lithospermum* (Boraginaceae), with an enumeration of the species and varieties. Two Canadian species are included, both being described as new; they are *L. cryptanthiflorum* (from Manitoba) and *L. boreale* (from Saskatchewan). The conspectus and descriptions are in Latin.

553. Rydberg, P. A. "Genera of North American Fabaceae. VII. *Astragalus* and Related Genera (continued)." *Amer. Journ. Bot.* **17**, pp. 231–238, Plates 16–17. 1930. (1. 150.)

The North American genera *Hamosa, Cystium, Onix, Geoprumnon, Hesperastragalus, Hesperonix,* and *Oxytropis* are described and illustrated. In addition, the two Old World

genera *Hedyphylla* and *Contortuplicata* are dealt with, these being represented in North America by introduced species.

554. Munz, P. A. "Studies in Onagraceae V. The North American Species of the Subgenera *Lavauxia* and *Megapterium* of the Genus *Oenothera*." *Amer. Journ. Bot.* **17**, pp. 358–370. 1930. (1. 151.)

The subgenera *Lavauxia* and *Megapterium* of *Oenothera* are represented in Canada by a single species, *O. flava* (a new combination based on *Lavauxia flava*). This species belongs to subgenus *Lavauxia* and ranges from Mexico northwards to Saskatchewan.

555. Evans, A. W. "Three Species of *Scapania* from Western North America." *Bull. Torr. Bot. Club*, **57**, pp. 87–111, Figs. 1–8. 1930. (1. 152.)

In this paper three species of *Scapania* (Scapaniaceae) from western North America are discussed from the standpoint of the ideas expressed by Buch in his recent treatise on the Scapanias of northern Europe and Siberia. *S. Bolanderi* and *S. americana*, two of the species dealt with by Evans, are plants of British Columbia.

556. Ostenfeld, C. H. and **Syrach Larsen, C.** "The Species of the Genus *Larix* and their Geographical Distribution." *K. Danske Videnskab. Selskab., Biol. Medd.* **9**, 2, pp. 1–107, Figs. 1–35, Maps 1–8. 1930. (1. 153.)

The authors deal in detail with the areas of distribution of the various species of *Larix* (Pinaceae). Of the ten species recognised three (*L. occidentalis*, *L. Lyallii*, and *L. laricina*) are American, and all these are found in Canada. A key to the species and varieties is given.

557. Woodson, R. E., Jr. "Studies in the Apocynaceae. I. A Critical Study of the Apocynoideae (with Special Reference to the Genus *Apocynum*)." *Ann. Missouri Bot. Gard.* **17**, pp. 1–212, Figs. 1–11, Plates 1–20. 1930. (1. 154.)

This includes a monograph of the exclusively North American genus *Apocynum*, of which seven species are recognised. In Canada *Apocynum* is represented by four species, all of which extend into the Dominion from the United States. The Canadian species are: *A. androsaemifolium* (type and var. *incanum*), *A. medium* (type and var. *sarniense*), *A. cannabinum* (vars. *pubescens* and *glaberrimum*), and *A. hypericifolium* (type and var. *salignum*). *A. medium* var. *sarniense* is a new combination based on *A. sarniense*.

558. Mathias, Mildred E. "Studies in the Umbelliferae. III. A Monograph of *Cymopterus* Including a Critical Study of Related Genera." *Ann. Missouri Bot. Gard.* **17**, pp. 213–476, Figs. 1–11, Plates 21–51. 1930. (1. 155.)

The group of genera dealt with is western North American with the exception of a single species which inhabits coastal eastern Asia. Four of the genera, *Musineon*, *Cogswellia* (*Lomatium*), *Glehnia*, and *Cymopterus*, are represented in Canada. Of these, *Musineon* and *Cymopterus* are fully monographed in the present paper. Their sole Canadian representatives are *M. divaricatum* var. *Hookeri* (a new combination based on *Musenium divaricatum* var. *Hookeri*) and *C. acaulis*, both of which range northwards from the western United States into south-western Canada.

559. Victorin, M. "Les Variations Laurentiennes du *Populus tremuloides* et du *P. grandidentata.*" *Contrib. Lab. Bot. Univ. Montréal,* **16**, pp. 1–16, Figs. 1–4. 1930. (1. 156.)

The Salicaceae hold a very important place in the Laurentian flora. Their ecological rôle is prominent in a country where the water resulting from heavy atmospheric precipitation is retained in the depressions of archaean rocks which are for the most part impermeable. But these plants command attention in another manner: they illustrate in the clearest possible fashion the behaviour of this flora of young and aggressive trees which, after the retreat of the pleistocene ice, has in recent times colonised the vast territory of the Laurentian system. This behaviour consists especially of an aptitude for giving rise to variations, more or less marked and more or less stable, which, if they are a source of embarrassment to the taxonomist, put the biologist on the track of the facts and achievements of evolution.

In the present paper the author deals with the variations of *Populus tremuloides* and *P. grandidentata* as they occur in the Laurentian region. Under *P. tremuloides* three new varieties (vars. *intermedia, rhomboidea,* and *magnifica*) and a new hybrid (*P. grandidentata* × *tremuloides*) are described, and a key is provided setting out the variations (including the hybrid) of *P. tremuloides* found in Quebec. Under *P. grandidentata* two varieties (vars. *angustata* and *subcordata*) are distinguished and proposed as new. The paper is in French.

560. Victorin, M. "Le Genre *Rorippa* dans le Québec." *Contrib. Lab. Bot. Univ. Montréal,* **17**, pp. 1–17, Figs. 1–8. 1930. (1. 157.)

In this revision the genus *Rorippa* (Cruciferae) is considered to be represented in Quebec by four species: *R. amphibia, R. sylvestris, R. obtusa,* and *R. palustris.* New combinations are proposed for three varieties and one forma, and in addition two formas of *R. palustris* are described as new. The paper is in French.

561. Victorin, M. "Some Evidences of Evolution in the Flora of North-eastern America." *Journ. of Bot.* **68**, pp. 161–172. 1930. (1. 158.)

The evidences are discussed under the headings of (*a*) Discontinuous Evolution and (*b*) Continuous Evolution. The author concludes that a comparative study of the flora of north-eastern America reveals several facts of first importance with respect to the question under consideration. These are:

(*a*) That this flora has gradually diverged from the flora of western America through isolation by an arm of the sea in Cretaceous times, and later on by the prairie which filled the sea bottom.

(*b*) That this flora has also gradually diverged from the North European flora through isolation by the disappearance during the Tertiary of the North Atlantic land bridge.

(*c*) That in the flora of north-eastern America, already modified by the above main causes of isolation, evolutionary advance has been fostered by two main processes—the stimulus of glacial action and the peculiar dynamism of estuarine conditions, both these processes amounting to physiological insularity.

562. Fernald, M. L. "The British Representatives of *Juncus tenuis.*" *Journ. of Bot.* **68**, pp. 364–367. 1930. (1. 159.)

Fernald here takes up S. F. Gray's name *Juncus macer* for the widely spread rush which formerly passed erroneously as *J. tenuis.* Michaux's name *J. bicornis,* which was adopted by K. K. Mackenzie for the same rush (see Abstract **391**), is considered by Fernald to be referable to the true *J. tenuis.* The new combinations *J. macer* var. *anthelatus* and *J. macer* var. *Williamsii* are proposed for two North American varieties.

563. Dearness, J. and **Sandford, G. B.** "A New Species of *Plenodomus.*" *Ann. Mycol.* **28**, pp. 324–325. 1930. (1. 160.)

A new species of fungus, *Plenodomus Meliloti*, is described. It is found in Alberta and Saskatchewan, and is parasitic on the living roots of *Melilotus*, *Medicago*, and *Trifolium*.

564. Zeller, S. M. and **Goodding, L. N.** "Some Species of *Atropellis* and *Scleroderris* on Conifers in the Pacific Northwest." *Phytopathology*, **20**, pp. 555–567, Figs. 1–2, Plate 1. 1930. (1. 161.)

Of the fungi dealt with in this paper one (*Atropellis pinicola*) is Canadian. This species, described as new under the new genus *Atropellis*, occurs in British Columbia and is associated with canker on living branches and trunks of *Pinus monticola* and *P. contorta*.

565. Vanterpool, T. C. "*Asterocystis radicis* in the Roots of Cereals in Saskatchewan." *Phytopathology*, **20**, pp. 677–680, Figs. 1–2. 1930. (1. 162.)

In Saskatchewan *Asterocystis radicis* has been observed frequently in the finer roots of oats, and occasionally in wheat, barley, and rye. It has also been found in the roots of maize, western rye grass (*Agropyron tenerum*), and field mustard (*Sinapis arvensis*).

566. Davidson, Jean E. "Notes on the Agaricaceae of Vancouver (B.C.) District—I." *Mycologia*, **22**, pp. 80–93. 1930. (1. 163.)

This includes a list of the known Agaricaceae of Vancouver District. Approximately 130 different species have been collected, but it has been impossible to identify all these with certainty. The list contains 81 species of whose identity there is no doubt. Genera and species are arranged in alphabetical order within each of the following spore groups: White-spored Group, Ochre-spored Group, Pink-spored Group, Purple-brown-spored Group, and Black-spored Group.

567. House, H. D. "A Collection of Plants from Point Abino, Ontario." *Can. Field-Naturalist*, **44**, pp. 117–119. 1930. (1. 164.)

The author gives a list of the seed plants and pteridophytes collected by F. W. Johnson at Point Abino, Welland County, Ontario, during the period 1921–6. Plants gathered by L. C. Davis at Port Maitland (Haldimand County) and at Turkey Point and Crystal Beach (Welland County) are also included in the list.

568. Vanterpool, T. C. and **Ledingham, G. A.** "Studies on 'Browning' Root Rot of Cereals. I. The Association of *Lagena radicicola* n.gen.; n.sp., with Root Injury of Wheat." *Can. Journ. Research*, **2**, pp. 171–194, Figs. 1–7, Plates 1–2. 1930. (1. 165.)

A specific root rot of wheat and other cereals is described, which is widespread over Saskatchewan and occasions severe losses in some regions. A fungus belonging to the lower Phycomycetes was found associated with rootlet injury of wheat, barley, rye, and maize seedlings grown in Regina clay soil from infested fields of southern Saskatchewan. This fungus is considered to represent a new genus of Ancylistaceae, and is described under the name *Lagena radicicola*. It is not regarded as one of the major causes of "browning" root rot, but in the section where it is common it is likely to be one of the contributory causes in some seasons.

569. Perry, F. "Ecological Notes on the Botany of the Coquihalla Area of British Columbia, Canada." *Mus. and Art Not. Vancouver*, **5**, pp. 7–11, 3 Figs. 1930: (1. 166.)

This comprises ecological notes made as the result of a visit paid in July 1929 to that part of the Coquihalla area (in southern British Columbia) bounded on the north by the Coquihalla River, on the south by the Iago Mountain, on the west by Hidden Creek, and on the east by Kelly Creek. The area visited is about 8 square miles in extent, and was entered by way of Tulameen Station, the route thence being up the Tulameen River (altitude 2561 ft.) 12 miles to Kelly Creek, then up Kelly Creek by trail to the west fork, the base camp being finally made at the foot of the Coquihalla Mountain at an altitude of 6200 ft.

570. Wailes, G. H. "Some Algae and Protozoa from Como Lake." *Mus. and Art Not. Vancouver*, **5**, pp. 26–27. 1930. (1. 167.)

A list is given including algae collected by members of the Burrard Field Naturalists' Club on July 7th, 1929, while on a visit to Como Lake, in the Coquitlam municipality, just outside the city limits of Vancouver.

571. Perry, F. "Ecological Notes on the Flora of the Bridge River District of British Columbia." *Mus. and Art Not. Vancouver*, **5**, pp. 150–159, 6 Figs. 1930. (1. 168.)

The ecological notes presented in this paper were made on a trip by the author in August 1930 to the Bridge River district of southern British Columbia by way of McGillivary Creek.

572. McAvoy, Blanche. "Successions in the Alpine Region of British Columbia." *Trans. Illinois St. Acad. Sci.* **22**, pp. 332–335. 1930. (1. 169.)

This is a brief study of plant successions in the alpine region of Canoe Crossing Mountain, a mountain bordering the northern side of the Bella Coola valley in the Coast Range of British Columbia. Canoe Crossing Mountain is somewhat less than 6000 ft. in height; the alpine region begins at an altitude of 4500 ft. above the floor of the Bella Coola valley.

573. Raup, Lucy C. "An Investigation of the Lichen Flora of *Picea canadensis.*" *The Bryologist*, **33**, pp. 1–11. 1930. (1. 170.)

The bark of trees offers a good substratum for lichens. Casual observation shows that there may be many different variations in this substratum and consequently in the lichen flora growing upon it. The present paper is a preliminary study of the distribution of lichens upon the white spruce (*Picea canadensis*). It is not a complete study, owing to the fact that it was impossible to carry on investigations over a long period of time and also since it was impossible to investigate the variations in light, heat, moisture, and air currents at various places on the trees. The work was done during the summer of 1927 whilst the expedition of which the author was a member was camped at the eastern end of Great Slave Lake, Mackenzie. For the purposes of the study two spruces, slightly different in size, were chosen. These were growing about 100 yards apart on an exposed peninsula, Fairchild Point, on the north shore of Great Slave Lake at its eastern extremity, this area being within 40 miles of the limit of trees which borders the great northern plains. The two trees were growing in very similar situations in relation to light, moisture, and exposure. After felling, each tree was measured and the trunk was divided into stations at intervals of 3 ft. At each of these stations the lichens were collected from the trunk, dead branches

and living branches. Records were kept of the relative abundance of the species represented, their distribution, and any variations that might appear in the size or form of any individual species. When the material was identified, the arbitrarily chosen stations were disregarded, and the associations and their limits worked out. In the paper the associations are described under the headings: (A) Lichen Associations on the Trunks, and (B) Lichen Associations on the Branches.

An annotated list of the species of lichen concerned is given at the end of the paper.

574. Raup, Lucy C. "The Lichen Flora of the Shelter Point Region, Athabasca Lake." *The Bryologist*, **33**, pp. 57–66, Plates 6–9. 1930. (1. 171.)

A collection of about 1200 specimens, representing about 80 species of lichens, was made by the author during the summer of 1926. This collection, gathered in the Athabasca Lake region of north-western Canada, furnished the material for the investigations recorded in the present paper. The purpose of the latter is to give a general discussion of the ecological distribution of the lichens within the Shelter Point region on the north shore of Athabasca Lake. An annotated list of the species collected was published in 1928 (see Abstract **234**).

The lichen flora of the Shelter Point region is described from an ecological standpoint, the associations being grouped as follows: (1) Terricolous and Saxicolous Associations on the Lake Shore, (2) Terricolous and Saxicolous Associations of the Upland, (3) Arboreal Associations, and (4) Terricolous Association of the Muskeg (a *Peltigera* Association).

575. Robitaille, A. "Végétaux Ligneux et Frutescents de la Région de Québec." *Naturaliste Can.* **57**, pp. 49–60, 73–79, 97–104, 121–130. 1930. (1. 172.)

The first part of this article takes the form of an alphabetical list of the woody seed plants considered to occur in the region of Quebec. The second part consists of a dichotomous key to the same plants, based on vegetative characters, particularly those of the leaves. The paper is in French.

576. Rousseau, J. "Notes sur les Mouvements Périodiques de Quelques Plantes." *Naturaliste Can.* **57**, pp. 109–112. 1930. (1. 173.)

Notes are given (in French) on the periodic flower movements of five species observed in Quebec: *Hieracium aurantiacum, H. Pilosella, Taraxacum officinale, Gentiana Victorinii*, and *Sisyrinchium angustifolium*.

577. Rousseau, J. "Les Entités Botaniques Nouvelles Créées par Brunet." *Naturaliste Can.* **57**, pp. 132–135. 1930. (1. 174.)

The several new names published by O. Brunet (1826–77), and generally ignored, are dealt with. A complete list of his publications, all dealing with Canadian botany, is given. The paper is in French.

578. Marie, L. "Étude sur les Potamots du Québec." *Naturaliste Can.* **57**, pp. 153–171, 4 Figs. 1930. (1. 175.)

A study (in French) of the genus *Potamogeton* in Quebec, including a key to the species and a descriptive enumeration of them.

(3) AUSTRALIA AND TASMANIA (COLLABORATOR, V. S. SUMMERHAYES)

579. Wood, J. G. "An Analysis of the Vegetation of Kangaroo Island and the Adjacent Peninsulas." *Trans. Roy. Soc. S. Australia, Adelaide,* **54,** pp. 105–139, 3 maps. Dec. 20th, 1930. (3. 41.)

In this paper an analysis is made of the flora and of the vegetation of Kangaroo Island and of the peninsulas of Fleurieu, Eyre and Yorke.

The flora of this Gulf Region is composed almost equally of migrant species from the western and eastern centres of distribution in Australia, together with 82 endemic species out of a total of 657. The distribution and affinities of the endemics is studied in further detail.

Life-form "spectra" computed according to Raunkaier's method are given for a number of areas and communities in the region under consideration. The vegetation of the district is then considered in greater detail under the following headings: (i) Fleurieu Peninsula; (ii) Kangaroo Island, (a) Mallee Scrub, (b) *Eucalyptus Baxteri-E. cosmophylla* Association on Lateritic Sands, (c) Heath Lands, (d) *Eucalyptus diversifolia-E. cladocalyx* Sub-climax Association; (iii) Southern Eyre Peninsula; (iv) Southern Yorke Peninsula.

Excluding the savannah forests of *Eucalyptus odorata* and *E. leucoxylon,* all the forest and scrub types developed within the 20-in. annual isohyet are of the sclerophyll type and are variants of the "Stringybark Formation" of the Mount Lofty Ranges, with *E. obliqua* as the climatic climax forest tree. A new edaphic sub-climax of this formation is recognised— the *E. diversifolia-E. cladocalyx* sub-climax—present in the west end of Kangaroo Island, in the Port Lincoln district, and in the southern extremity of Yorke Peninsula. Other sub-climaxes and associations are recognised, and their relations to the succession shown in the sclerophyll forests of southern Australia are discussed.

A vegetation map of the forests of southern Australia is included in the paper.

A list of all the species found in the area, with their growth forms and more detailed distribution is provided.

580. Sargent, O. H. "Xerophytes and Xerophily, with Special Reference to Protead Distribution." *Proc. Linn. Soc. New South Wales,* **55,** pp. 577–586. Sydney, Dec. 15th, 1930. (3. 42.)

Although the species of the family Proteaceae seem to have such marked xerophilous structure yet they are not found in arid districts, but in the damper coastal districts of extra-tropical Australia. Transpiration experiments show that loss of water is great especially from flowering branches, and flowering nearly always takes place during the dry summer. The great majority of Proteads therefore need to live in areas with at least 30 in. annual rainfall. Where species occur in areas of less rainfall they are often associated with underground water supplies or similar ameliorating influences. Experiments showed that the needle leaves of *Hakea trifurcata* transpire more actively than the broad lanceolate leaves of the same species, and observations indicated that broad leaves are only found on shrubs in areas with little rainfall. The author is of opinion that internal properties determine whether the species can live in dry places, and not the outer structure (xerophilous devices, etc.).

581. MacGillivray, W. D. K. and **Rodway, F. A.** "Plants on Islands of the Bunker and Capricorn Groups." *Reports of the Great Barrier Reef Committee,* Government Printer, Brisbane, **3,** No. 7, pp. 58–63. Jan. 13th, 1931. (3. 43.)

The island groups visited lie off the coast of Queensland between 23° and 25° S. lat. Altogether nine islands were visited, and short descriptions of the vegetation in each case is given. A list of all the species recorded is also provided.

582. Lucas, A. H. S. "The *Caulerpas* of Victoria." *Victorian Naturalist, Melbourne*, **48**, pp. 84–93, 2 plates. Sept. 8th, 1931. (3. 44.)

Sixteen species are recorded as occurring in Victoria. A synopsis of the species is given together with short descriptions and the distribution in each case. Six of the species are figured.

583. Barrett, A. O. and **Green, H.** "The Seasonal Sap Flow of *Eucalyptus botryoides*." *Proc. Roy. Soc. Victoria, Melbourne*, **43**, pp. 241–250. Feb. 28th, 1931. (3. 45.)

The roots of mature trees of *Eucalyptus botryoides* are apparently dormant during spring and summer, but begin to form active roots in the early autumn. During the autumn and winter water is stored up in the bark, the moisture content of the living bark rising from 57 to 64 per cent., whilst the formation of new leaves is almost nil. After the period of rains the new leaves form in groups every 3–5 weeks throughout the spring and summer.

It seems probable that the above and other peculiarities are some of the developments which have enabled Eucalypts to flourish in a semi-arid climate, withstanding a summer drought and storing up a water supply in the wet season.

(4) NEW ZEALAND (Collaborator V. S. Summerhayes)

584. Speight, R. "The Lake Ellesmere Spit," with Appendix on Plant Covering by **A. Wall.** *Trans. New Zealand Institute, Wellington*, **61**, pp. 147–169, Plates 27–33, 1 map, 2 sections. 1930. (4. 33.)

The topography, structure and geology of the spit are described together with a discussion of its origin. Two types of habitat occur, namely (1) sand-dunes nearer the sea, on which *Poa caespitosa* is dominant, except in the immediate seaward zone where *Scirpus frondosus*, *Carex pumila* and *Calystegia Soldanella* replace it, while a number of shrubs are found on the highest ridge; and (2) beach of loose stones, supporting a vegetation like that of great river beds.

585. Wild, G. V. and **Zotov, V. D.** "Notes on Sexual Expression in Certain Species of New Zealand Coprosmas." *Trans. New Zealand Institute, Wellington*, **60**, pp. 547–555, 3 Text-figs. March 31st, 1930. (4. 34.)

Although the flowers in the genus *Coprosma* are normally dioecious, in a number of species hermaphrodite flowers have been noticed. A list of these is given with notes on their occurrence.

586. Laing, R. M. "A Reference List of New Zealand Marine Algae, Supplement 1." *Trans. New Zealand Institute, Wellington*, **60**, pp. 575–583. March 31st, 1930. (4. 35.)

In this supplement 16 new species are added, 7 species are removed from the original list, while 27 changes in nomenclature are recorded.

587. Laing, R. M. and **Gourlay, H. W.** "The New Zealand Species of *Gigartina*, Part 1." *Trans. New Zealand Institute, Wellington*, **60**, pp. 102–135, Plates 5–15, 26 Text-figs. May 31st, 1930. (4. 36.)

The present paper only deals with those species without broadly expanded laminae. These number 18, but as little collecting has been done on the west coast the account really only deals with the east coast species. A synopsis of the sections and species is given, followed by detailed descriptions together with drawings and photographs.

588. Cockayne, L. and **Teichelmann, E.** "The Glacial Scenic Reserves of Westland." Append. C to the *Annual Report on Scenery Preservation* for the year ended March 31st, 1930, Department of Land and Survey, New Zealand, pp. 1–11, frontispiece and 11 photographic figs., 1 map. W. A. G. Skinner, Government Printer, Wellington, 1930. (4. 37.)

The four reserves described embrace the glaciers and snowfields on the western side of the main Divide of the Southern Alps between the Callery and Twaine Rivers together with the mostly forest-clad country below.

An account of the flora is given with descriptions of some of the more interesting species. The vegetation can be divided into the following main classes: (1) forest associations; (2) swamp communities; (3) shrub associations; (4) rock vegetation; (5) subalpine herb field; (6) alpine associations confined to débris.

The lowland forests are dominated by *Weinmannia racemosa* together with species of *Podocarpus* and *Dacrydium*. The chief tree of the montane-lower subalpine forest is *Metrosideros lucida* together with *Weinmannia*. Short notes are given of the more alpine communities. A short account is given of the establishment of vegetation on areas left exposed by the retreating glaciers. Finally, a list is supplied of all the species so far recorded.

(5) PACIFIC ISLANDS (COLLABORATOR V. S. SUMMERHAYES)

589. Dixon, H. N. and **Greenwood, W.** "The Mosses of Fiji." *Proc. Linn. Soc. New South Wales, Sydney*, **55**, pp. 261–302, Plates 8–9. July 15th, 1930. (5. 9.)

The number of known Fiji mosses now stands at 205, which is probably about half of the total number. Very few of the mosses are found below 1000 ft. (300 m.) on the dry side of the islands, which has been most studied by Mr Greenwood. A key to the genera is given, while records of all species, with notes, follow. Twenty-seven new species are described.

(6) MALAYA AND EAST INDIES (COLLABORATOR C. V. B. MARQUAND)

590. Enriques, C. M. *Kinabalu; the haunted mountain of Borneo*; an account of its ascent, its people, Flora and Fauna: 199 pp. (8vo.) with photographs and a map. H. F. and G. Witherby, London, 1927. (6. 11.)

One appendix of seven pages is devoted to the "Botany of Kinabalu." In this necessarily brief account the principal species of flowering plants are mentioned and some reference is made to the associations comprising the vegetation. No complete enumeration of the Phanerogamia is made but, at the end of the chapter, a list of the Bryophyta is given. This includes eleven species of which one (*Dicranoloma angustifrondum* Dixon) is a new species.

591. Foxworthy, F. W. and **Woolley, H. W.** "Durability of Malayan Timbers." *Malay Forest Records*, No. 8, 1–44 (1930). (6. 12.)

592. Lauterbach, C. "Die Pflanzenformationen einiger Gebiete Nordost-Neu-Guineas und des Bismark-Archipels." I, *Englers Bot. Jahrb.* **62**, 284–304. 1928; II, *loc. cit.* 550–569. 1929; III, *loc. cit.* **63**, 1–28. 1929; IV, *loc. cit.* 419–476. 1930. (6. 13.)

This is Part xv of Prof. Lauterbach's "Beiträge zur Flora von Papuasien." In addition to the Enumeration of the Flora it comprises a complete account of the vegetation of this region as well as much introductory matter on the climatic and other factors controlling it. Since the area lies just outside the British Empire it cannot be summarised here, reference being made to this series of papers merely on account of their importance in relation to the adjoining areas of British New Guinea.

593. Pendlebury, H. M. "A Note on Termites." *Malay Forest Records*, No. 8, 45–56 with Plates 1–6. 1930. (6. 14.)

A general account of the life-history of the Termites is given as well as a brief account of the species most commonly met with in the Federated Malay States and a list of the 74 species which have been recorded with reference to their place of publication.

(7) INDIA, BURMA AND CEYLON (COLLABORATOR, R. J. D. GRAHAM)

594. Shebeare, E. O. "The Malatas of Northern Bengal." *Indian Forester, Allahabad*, **56**, pp. 1–5, Plate 1. Jan. 1930. (7. 101.)

Cowan's key (see **441**) and illustrations of the leaves on which the key is based are criticised. Six *Malatas* are described with illustrations and are provisionally identified as *Mallotus Roxburghianus, M. albus, M. nepalensis* and *Macaranga pustulata, M. denticulata* and *M. indica*.

595. Bell, J. L. "The East Khandesh Forest Division, Bombay Presidency." *Indian Forester, Allahabad*, **56**, pp. 17–21. Jan. 1930. (7. 102.)

A description of the climate and geology of an area situated on the Tapti river.

596. Parker, R. N. "Three new Spiraeas from the N.W. Himalaya." *Indian Forester, Allahabad*, **56**, pp. 105–108, Plate 20. March, 1930. (7. 103.)

A key to the Spiraeas of the section Chamaedryon found in the Himalaya west of the Nepal border is given. *S. lycioides, S. affinis, S. hazarica* are described as new species.

597. Davis, D. "A descriptive account of the Bahraich Forest Division, U.P." *Indian Forester, Allahabad*, **56**, pp. 108–115, Plate 21. March, 1930. (7. 104.)

An area in the north of the United Provinces bordering on Nepal is described.

598. Hamilton, J. D. "Teak Bearing Rocks." *Indian Forester, Allahabad*, **56**, pp. 147–156. April, 1930. (7. 105.)

The association of good Teak in Burma with lime in the soil is described. Other trees which show marked benefit from abundance of lime are *Xylia dolabriformis, Terminalia*

tomentosa, Acacia Catechu, Millettia spp., *Lagerstroemia* spp., *Eugenia* spp., *Melanorrhoea* sp., *Mangifera caloneura, Stephegyne diversifolia, Dillenia* spp., and *Tectona Hamiltoniana.*

599. Ford–Robertson, F. C. "Kalagarh Forest Division." *Indian Forester, Allahabad,* **56**, pp. 164–171. April, 1930. (7. 106.)

An account of an area of 400 square miles of rugged foothills occupying the main drainage area of the Ramganga. The steep southern slopes carry mixed deciduous trees of xerophytic type. Pure dense *Sal* occupies the flats and river terraces, a transition at the governance of slope and aspect that forms an object-lesson in simple oecology.

600. Allsop, F. "*Gmelina* plantations at the Bawdwin Mines." *Indian Forester, Allahabad,* **56**, pp. 203–211, Plate 27. May, 1930. (7. 107.)

The problem of supplying 20,000 tons of timber annually in the Shan hills. Experiments with *Eucalyptus species* and *Cedrela Toona, Chickrassia tabularis* and *Gmelina arborea* were undertaken. White ants militated against the *Eucalyptus* but *Gmelina arborea* proved satisfactory.

601. Smythes, E. A. "The Sal Forests of Haldwani, North Kheri and Nepal." *Indian Forester, Allahabad,* **56**, pp. 243–250. June, 1930. (7. 108.)

Haldwani and North Kheri possess the finest *Sal* forests in the United Provinces. A comparison is drawn between these and those of Nepal particularly with regard to regeneration which takes place naturally in Nepal.

602. Hopkins, G. M. "Chakrata Forest Division." *Indian Forester, Allahabad,* **56**, pp. 250–253. June, 1930. (7. 109.)

The forests in the north-west corner of Dehra Dun District consist of (1) a subtropical or Sal Kohat Zone to 3000 ft., (2) a temperate or Chir Zone from 3000 to 6000 ft., (3) a subalpine or Deodar Zone from 6500 to 9000 ft., and (4) an Alpine Zone above 9000 ft.

603. David, A. M. "Seraj Forest Division." *Indian Forester, Allahabad,* **56**, pp. 299–302, Plate 30. July, 1930. (7. 110.)

An account of an area in the Kulu Division at elevations from 3000 to 18,000 ft. The main trees are *Cedrus Deodora, Pinus excelsa, P. longifolia, Picea Morinda, Abies Webbiana* and *A. Pindrow.*

604. Shebeare, E. O. "Fire and Sal Regeneration." *Indian Forester, Allahabad,* **56**, pp. 302–306. July, 1930. (7. 111.)

After a comparison of a Sal area in Bengal, where artificial regeneration is the rule, with a Sal area in Assam where natural regeneration holds, a method of natural regeneration through burning is outlined.

605. Flewett, W. E. "A short account of the Kulu Forest Division." *Indian Forester, Allahabad,* **56**, pp. 334–339, Plates 30 and 31. Aug. 1930. (7. 112.)

A descriptive account of an area adjacent to Seraj (603).

606. Parkinson, C. E. and **Raizada Mukat Behari.** "New Indian Species of Forest Importance. Part I." *Indian Forester, Allahabad,* **56,** pp. 426–440. Oct. 1930. (7. 113.)

Enumerates 218 species described since 1924.

607. Augier, P. W. "Musings on the Pari Forest Division." *Indian Forester, Allahabad,* **56,** pp. 471–481. Nov. 1930. (7. 114.)

An account of a portion of the forests in Bihar and Orissa. *Webera corymbosa* and *Thysanolaena agrostis* are stated to indicate areas where natural regeneration of *Sal* may be expected.

608. Tadulingham, C. and **Jacob, K. Cheriyam.** "A new species of *Senecio*." *Journ. Ind. Bot. Soc. Madras,* **9,** pp. 40–41, Plates 1 and 2. March, 1930. (7. 115.)

Senecio Ansteadi allied to *S. corymbosus* is described from South India.

609. Borgensen, F. "Some Indian Green and Brown Algae especially from the shores of the Presidency of Bombay." *Journ. Ind. Bot. Soc. Madras,* **9,** pp. 151–174, Plates 1 and 2, Text-figs. 10. July, 1930. (7. 116.)

Nine green algae and eight brown collected during a few months in 1927–8 are identified. One new genus of green *Willeella* represented by *W. ordinata* and one new species *Pseudobryopsis mucronata* are described.

610. Miller, J. H. and **Tandon, R. N.** "The Fungus Flora of Allahabad." *Journ. Ind. Bot. Soc. Madras,* **9,** pp. 190–198. Oct. 1930. (7. 117.)

A list of 84 fungi collected in the fields, gardens and parks of Allahabad town.

611. Blatter, E. "Plantae Novae Waziristanensis." *Journ. Ind. Bot. Soc. Madras,* **9,** pp. 199–207. Oct. 1930. (7. 118.)

Descriptions of 14 new plants collected by J. Fernandes in March to June 1927. These included *Ranunculus nanus, R. echinatissimus, Viola oblonga, Althaea villosa, A. villosoides, Malva waziristenensis, Oxalis foliosa, Trigonella dimorpha, T. longe-pedunculata, Argyrolobium strigosum, Caragana spinosissima, Prunus leucophylla, Pyrus parviflora.*

612. Skvortzow, B. W. "Notes on Ceylon Diatoms. I." *Ann. Roy. Bot. Gard. Peradeniya, Ceylon,* **11,** pp. 251–259, Plates 32–34. Jan. 1930. (7. 119.)

A list of 99 forms collected in five localities in Ceylon. Twenty-six new forms are described in the list.

613. Petch, T. "Buttress Roots." *Ann. Roy. Bot. Gard. Peradeniya, Ceylon,* **11,** pp. 277–285, Plates 35–38. Jan. 1930. (7. 120.)

The buttress roots on *Bombax malabaricum, Poinciana regia, Canarium commune, Ficus elastica* and *Terminalia Catappa,* are described and illustrated by photographs. The writer puts forward as a working hypothesis (1) that the presence of buttress roots is associated with a deficient tap root, and (2) that the formation of buttress roots is due to the restriction of the food and water currents to limited narrow regions of the stem continuous with the lateral roots.

614. Millard, W. S. and **Blatter, E.** "Conspicuous Flowering Trees of India." *Journ. Bombay Nat. Hist. Soc.* **33**, pp. 624–635, Col. Plates 1 and 2, Plates 1 and 2, Text-figs. 5; pp. 852–856, Col. Plates 3 and 4, Plates 3 and 4, Text-figs. 5. 1929. **34**, pp. 83–86, Col. Plates 5 and 6, Plates 5 and 6, Text-figs. 4; pp. 271–275, Col. Plates 7 and 8, Plates 7 and 8, Text-figs. 5; pp. 716–719, Col. Plates 9 and 10, Plates 9 and 10, Text-figs. 5. 1930. (7. 121.)

The trees chosen for illustration are *Erythrina indica, Bombax malabaricum, Poinciana regia, Butea frondosa, Guaiacum officinale, Millingtonia hortensis, Plumieria acutifolia, P. rubra, Thespesia populnea, Spathodea campanulata, Peltophorum ferrugineum.*

615. Biswas, K. P. "Contribution to our knowledge of the fresh water Algae of Manipur, Assam." *Journ. Bombay Nat. Hist. Soc.* **34**, pp. 189–192, Plates 1–3. March, 1930. (7. 122.)

Five species are described including a new variety *Spirogyra setiformis* v. *major.*

616. Fernandez, J. "A list of Mosses from Darjeeling district." *Journ. Bombay Nat. Hist. Soc.* **34**, pp. 600–601. July, 1930. (7. 123.)

An alphabetical list of 26 mosses collected at elevations of 6000 to 8200 ft. The identifications are by H. N. Dixon.

617. Sethi, R. L. "Root Development in Rice under different conditions of Growth." *Memoirs Dept. Agric. India, Bot. Series, Calcutta,* **18**, No. 2, pp. 57–80, Plates 1–3, Text-figs. 3. Feb. 1930. (7. 124.)

A method for excavating root systems is described. Two types of roots are noticed.

618. Trought, T. and **Afzal Mohammad.** "Cotton growing in India in relation to climate." *Memoirs Dept. Agric. India, Bot. Series, Calcutta,* **18**, No. 5, pp. 117–136. Dec. 1930. (7. 125.)

The climatic factors which are treated separately include temperature (maximum and minimum) and moisture (rainfall, rainy days, cloud, humidity, wind).

619. Borgensen, F. "Fra en rejse i Indien, 1927–28." *Botanisk Tidsskrift,* **41**, pp. 113–153, Text-figs. 15. 1930. (7. 126.)

An account of a botanical journey from Bombay through Dharwar to Madras, thence to Tuticorin. Thirty-five species collected at Tuticorin are enumerated and comparison drawn with sandy shore vegetation of other countries. Here therophytes reach 37 per cent., chamaephytes 28·5 per cent. and phanerophytes only 23 per cent.

620. Ward, F. Kingdon. *Plant Collecting on the Edge of the World.* Victor Gollancz, Ltd., London, pp. 383, with 16 plates and 3 maps. Aug. 1930. (7. 127.)

The volume deals with an area situated on the northern frontier of Burma including the Mishmi Hills and records the observations made on two plant-collecting journeys. Access to the collecting ground was obtained from North Burma on the first trip. The area traversed

is a portion of the divide between the western and eastern branches of the Irrawady. By crossing to the Lohit River through the Mishmi Hills the first episode is successfully terminated. After an interval, a second expedition is made from Assam, to the Delei Valley.

Both journeys occupied six months. The two collecting grounds were situated only 75 miles apart, yet each yields very different results.

The more prominent geographical and floristic features are set out with observations on the distribution and character of the vegetation. Prominent members of the flora are more fully detailed.

(9) TROPICAL AMERICA AND WEST INDIES (COLLABORATOR, R. C. MCLEAN)

621. Nicholson, E. M. "In the Guiana Rain Forest." *The Times*, October 15th, 1929. (9. 11.)

Popular account of the preliminary work of the Oxford Expedition, 1929, in the forest on Moraballi Creek.

622. Williams, R. O. *Flora of Trinidad and Tobago.* **1**, Pt 3. Olacales, Celastrales, Sapindales. Pp. 165–196. Nov. 1930. (9. 12.) The Department of Agriculture, Port of Spain, Trinidad.

Predominantly arboreal families, important forest constituents. The species covered are mostly of local distribution or endemic. Two new species, *Ilex arimensis* and *Maytenus monticola* are described.

623. Marshall, R. C. *Notes on the Silviculture of the more important Timber Trees of Trinidad and Tobago.* 8vo. pp. 47 and Index. 6 plates. Forest Dept., Trinidad and Tobago. Trinidad. 1930. (9. 13.)

Chapter I deals in brief outline with the ecological characteristics of the forest timber-trees, i.e. soil relationships, growth rates, forest climates, etc. Chapters II and III are purely forestry, dealing with establishment of plantations and the treatment of forest. Chapter IV deals in detail with the taxonomy, reproduction, products and culture of the chief forest trees, in systematic order. The plates illustrate forest vegetation.

624. Follett Smith, R. R. "The Report of the Investigation of the Soils and Mineral Content of Pasture Grasses at Waranama Ranch, Berbice River." *Agric. Journ. Brit. Guiana*, **3**, pp. 142–160, 4 illus., 1 map. Georgetown. 1930. (9. 14.)

The soil of the savannah consists mostly of acidic sands. (*a*) Sand Hill Type. Light to dark grey, with loss on ignition of 3·5 to 7·7 per cent. Bears savannah. (*b*) Brown Sand Type, with up to 2·7 per cent. of ferric oxide, merging at 2 ft. depth into heavy red-brown loam. Loss on ignition 3·9 to 4·5 per cent. Bears savannah. (*c*) Muri Sand Type. Over 99 per cent. pure silica. Colour white. Very slight amount of organic matter at surface. Bears xerophytic bush.

625. Young, P. V. "Timbers of British Guiana." *The Empire Review*, **51**, pp. 49–53. 1930. (9. 15.)

A popular account of the more important forest timbers and their uses, with a special plea for the more extensive use of Mora for railway sleepers in Britain.

BRITISH EMPIRE VEGETATION ABSTRACTS:

TITLES AND ABSTRACTS OF PUBLICATIONS ON THE VEGETATION AND ECOLOGY OF THE OVERSEAS EMPIRE AND ON RELATED TOPICS

(2) SOUTH AFRICA (COLLABORATOR, A. W. EXELL)

626. Phillips, E. P. "An Introduction to the Study of the South African Grasses with Notes on their Structure, Distribution, Cultivation, etc." *S. Afr. Agric. Ser.* **6**, pp. 1–224, Plates 1–121, Figs. 1–5. 1931. (2. 103.)

This important account of the South African grasses in addition to a systematic account of the genera, accompanied by a key and copiously illustrated, contains three short chapters of ecological importance. In dealing with migration and distribution the author divides the genera into five groups: I. Genera belonging to tropical and temperate tribes distributed in the Transvaal and southward through the eastern and south-eastern coastal belt, and extending westward into the south-western districts. Examples: *Eulalia, Eleusine, Trachypogon, Koeleria, Tristachya, Holcus, Phalaris, Leersia, Oplismenus.* II. Northern genera mostly confined to the Transvaal, but occasionally entering Natal. Examples: *Lophachme, Dinebra, Tripogon, Urelytrum, Eriochrysis.* III. Genera of tropical origin which have extended from the Transvaal through the eastern districts and entered the south-western districts, and have also migrated westward to the north-western and central districts. Examples: *Eragrostis, Cymbopogon, Hyparrhenia, Heteropogon, Themeda, Panicum, Brachiaria, Digitaria, Pennisetum.* IV. A group of genera of northern origin which have extended westward from the Transvaal. A few extend southwards to Natal or further but none beyond Port Elizabeth. Examples: *Alloteropsis, Schizachyrium, Rhaphis, Dichanthium, Anthephora, Schmidtia, Triraphis, Pogonarthria, Xyochlaena.* V. Temperate genera typical of the south-western districts not extending beyond East London in the coastal belt but extending northwards along the tops of the high mountains, sometimes as far as northern Transvaal. Examples: various genera belonging to the Tribes *Aveneae, Festuceae* and *Hordeae.* In South Africa there have apparently been three lines of migration. (1) The temperate genera northward along the mountain ranges and surviving on isolated mountains. (2) The tropical genera southward along the valleys, thus populating the eastern belt and extending into the south-western districts. (3) A westward migration of tropical grasses into the north-western area and the Karroo generally.

The distribution of the genera in the various districts of the Union is given in detail as far as records are available. The temperate grass flora of the south-western districts is found to have a large number of genera in common with other temperate countries such as North America, Australia and New Zealand. There is also considerable affinity with the grasses of India again with reference to the south-western area. The ecology of the grass veld is dealt with from the point of view of veld burning, grazing and mowing.

627. "Novitates Africanae." *Journ. of Bot.* **69**, pp. 10–15, 48–50, 207–211 and 258–262. 1931. (2. 104.)

Descriptions of new species in the genera *Liriothamnus* and *Crassula* by R. H. Compton, in the genera *Oxalis, Homeria, Syringodea, Romulea, Hesperantha, Antholyza, Ferraria, Watsonia* and *Gladiolus* by L. Bolus, in the genus *Gamolepis* by N. S. Pillans and in the genus *Oxalis* by D. Weintroub.

628. Smith, C. A. "A New *Harveya* from the Transvaal Highveld." *Bull. Misc. Inf. Kew*, pp. 65–67, Plates IV–V. 1931. (2. 105.)

This new species, *H. anisodonta*, is a root parasite which apparently confines itself to the Compositae.

629. "Decades Kewenses." *Bull. Misc. Inf. Kew*, pp. 98 and 100–102. 1931. (2. 106.)

New species are described by C. A. Smith in the genera *Coelidium* and *Eriocephalus*.

630. Brown, N. E. "Notes upon South African Plants." *Bull. Misc. Inf. Kew*, pp. 191–197. 1931. (2. 107.)

New species of *Aristea*, *Watsonia*, *Morea* and *Bulbine* are described.

631. Herre, H. "Eine Sammelreise nach Namaqualand." *Monatsschr. Deutsch. Kakteen-Gesell.* **3**, pp. 1–12 and 25–36, 12 Photographs. 1931. (2. 108.)

An account of a collecting trip to Namaqualand with special reference to the succulents and their habitats.

632. Verdoorn, I. C. "*Huernia Nouhuysii* sp.nov." *Flowering Pl. S. Afr.* **11**, Pl. 412. 1931. (2. 109.)

633. Bolus, L. "*Homeria Galpinii* sp.nov." *Flowering Pl. S. Afr.* **11**, Pl. 417. 1931. (2. 110.)

634. Barker, W. "*Polyxena Maughanii* sp.nov." *Flowering Pl. S. Afr.* **11**, Pl. 420. 1931. (2. 111.)

635. Bews, J. W. and **Bayer, A. W.** "Researches on the Vegetation of Natal—Series III. Section I. On the Reaction of *Digitaria eriantha* var. *stolonifera* (Stapf) and *Themeda triandra* (Forsk.) to the Winter Season." *S. Afr. Journ. Sci.* **28**, pp. 158–168, Text-figs. 1–4. 1931. (2. 112.)

The influence of the winter season upon the nitrogen and carbohydrate mechanism of *Digitaria eriantha* var. *stolonifera* Stapf and *Themeda triandra* Forsk. was investigated and in both plants the protein content varies directly with the water content and decreases with the approach of winter, while pentosan content varies inversely with the water content and increases with the approach of winter.

636. Osborn, J. B. "Some Physical Properties of the Wattle Soils of Natal." *S. Afr. Journ. Sci.* **28**, pp. 207–221. 1931. (2. 113.)

A description is given of standard types of soils existing in the principal wattle-growing areas of Natal and their physical properties are correlated with their productivity under wattles. It is difficult to differentiate between the effect of the soil and that of the climate in that the climate itself has been the dominating factor in the production of a given soil type. There is, however, a definite relationship between the physical properties of the soil of a given type and its productivity, so that knowledge of the physical properties of the various types of wattle soils is essential to the understanding of problems relating to burning and cultivation.

637. Schonken, J. D. "Plant Life and the Siccation Process." *S. Afr. Journ. Sci.* **28**, pp. 238–245, 1 Text-fig. 1931. (2. 114.)

The processes of desiccation (diminution of rainfall) and exsiccation (drying out of the earth's crust and the atmosphere) are clearly to be differentiated. Deforestation scarcely affects the former but definitely affects the latter with deleterious results in South Africa.

638. Sim, T. R. "Further Notes on the Distribution of the Ferns of South Africa." *S. Afr. Journ. Sci.* **28**, pp. 253–265. 1931. (2. 115.)

This consists of addenda to the author's *Ferns of South Africa*, giving changes in the known areas of distribution of the species.

639. Dippenaar, B. J. "Descriptions of some New Species of South African Fungi and of Species not previously recorded from South Africa. II." *S. Afr. Journ. Sci.* **28**, pp. 284–289. 1931. (2. 116.)

New species of *Phoma, Gloeosporium, Phyllosticta, Septoria, Heterosporium, Stagnospora, Mycosphaerella, Pleospora, Puccinia* and *Aecidium* are described.

640. Verwoerd, L. and **du Plessis, S. J.** "Descriptions of some New Species of South African Fungi and of Species not previously recorded in South Africa. III." *S. Afr. Journ. Sci.* **28**, pp. 290–297. 1931. (2. 117.)

New species of *Cryptostictis, Gloeosporium, Macrophoma, Phyllosticta, Pleospora, Septogloeum, Septoria* and *Sphaerulina* are described.

641. Verwoerd, L. "A Preliminary List of Fungi from the Bloemfontein District of the Orange Free State." *S. Afr. Journ. Sci.* **28**, pp. 298–301. 1931. (2. 118.)

642. Fantham, H. B. "Some Protozoa in certain South African Soils. X." *S. Afr. Journ. Sci.* **28**, pp. 334–343. 1931. (2. 119.)

This deals with soils from the Caledon area, from Salisbury Island, and from the Kalahari.

643. Sim, T. R. "South African Bryophyta. Further Notes." *Trans. Roy. Soc. S. Afr.* **20**, pp. 15–31. 1931. (2. 120.)

Additions to records of distribution of South African *Bryophyta*. Table Mountain species are found to extend across into the Hottentots' Holland and Swellendam Mountains, and the Western Karroo species are found to extend more widely than at first appeared.

644. Nygaard, G. "Contributions to our Knowledge of the Fresh-water Algae of Africa. 9. Fresh-water Algae and Phytoplankton from the Transvaal." *Trans. Roy. Soc. S. Afr.* **20**, pp. 101–148, Figs. 1–48. 1932. (2. 121.)

In the Transvaal the plankton and more especially the algal flora are exposed to extraordinarily great daily and annual oscillations of temperature. The shallow lakes and ponds (e.g. the "pans") may cool down in winter nights to temperatures not much above freezing point, while in summer they may reach day temperatures not far from 30° C. The localities are divided into four groups: (1) Artificial dams—of little botanical interest. (2) Semi-natural

lakes. These are streams dammed at one end and have rather low mineral content. *Batracho-spermum* occurs in the streams. Reed swamps are present, floating leaved plants are found, and submerged plants are not rare. There is a moderately rich plankton. (3) Natural pans. The pans are shallow depressions, perhaps caused by wind. Some always contain water: others dry up in winter, in which case the mineral content becomes very high as the water evaporates. *Zannichellia*, *Potamogeton pectinatus* var., etc., occur in these pans, and also *Lemna minor*, *Lemna gibba* and *Wolffia arhiza*. *Potamogeton Livingstonei* A. Bennett occurs in Lake Chrissie, which does not dry up. The plankton of these natural pans is rich, especially after the early seasonal rains. (4) River dams. The River Vaal has been dammed at Vereeniging. The *p*H is around 7·9 and the mineral content is high. When the summer rains commence the plankton must be largely washed away: in the winter it is very abundant—chiefly Copepods and Diatoms.

The plankton in the natural pans is a typical pond plankton, mainly consisting of organisms that must be designated as more or less littoral. It is characterised by *Volvox Rousseletii* West, *Microcystis aeruginosa* Kg. and the ubiquitous *Botryococcus Braunii* Kg. which is sometimes dominant. Besides these the plankton consists mainly of Chlorophyceae. The plankton of the semi-natural lakes and river dams is dominated by the Diatom *Melosira*. Samples from Florida Lake, Vaal River Dam, and Rietkuil are the only ones containing genuine plankton organisms such as those which make up the plankton of larger bodies of water. The *Melosira-Anabaena* association found in Lake Nyasa also occurs in Rietkuil.

The comparative paucity of Desmids is noteworthy. In general the lake plankton of the Transvaal is not rich in species and the same applies to the pond plankton. The most interesting organisms are to be found in the natural pans, where extreme life conditions exist. The lakes, on the other hand, bear a much more cosmopolitan stamp.

New species of *Calothrix*, *Coscinodiscus*, *Ulothrix*, *Oedogonium*, *Closterium* and *Spirogyra* are described.

645. Rich, Florence. "Contributions to our Knowledge of the Fresh-water Algae of Africa. 10. Phytoplankton from South African Pans and Vleis." *Trans. Roy. Soc. S. Afr.* **20**, pp. 149–188, Figs. 1–20. 1932. (2. 122.)

The pans or vleis are shallow, circular or kidney-shaped depressions, usually with no outlet, or only a temporary one, and varying from a few yards across to several square miles. They may or may not dry up during the dry season. Those that on drying leave a rich terrestrial vegetation are known as Grass Pans, while those that do not leave much vegetation are styled Mud Pans. The hydrogen-ion concentration varies from *p*H 6·7 to *p*H 9·2 and the salinity is very variable. The phytoplankton is in general poor, a noteworthy exception being the Weltevreden West Pan which has pure, clear, slightly acid water and in which a great number of species and varieties occur. The blue-green Algae are plentiful where salinity is high; they also occur with low salinity; but they are not found where phosphate content is high. New species of *Closterium*, *Cosmarium*, *Staurastrum* and *Aphanothece* are described.

646. Huber–Pestalozzi, G. "Das Plankton natürlicher und künstlicher Seebecken Südafrikas." *Atti del Congr. Intern. di Limnologia*, 1927, **4**, pp. 343–390, Text-figs. 1–6. 1929. (2. 123.)

Two types of water are distinguished: vleys and dams. The vleys differ in the water being more stagnant and more muddy and in the fact that they frequently dry up. The phytoplankton is much poorer and atypical while that of the dams is richer and typical. The dams lack such zooplankton as *Leydigia*, *Moina*, *Daphnia pulex* and *D. magna* which are

frequently found in the vleys. More Ostracods are also to be found in the vleys. The general conclusion is that the plankton flora and fauna of South African pools, natural or artificial, agrees in the main with that of Central Europe. There are, however, a number of local races and some endemic species which give the plankton a South African facies. New species and specific combinations are published in the genera *Croococcus*, *Actinastrum*, *Staurastrum*, *Anuraea* and *Mesocyclops*.

647. Huber-Pestalozzi, G. "Algen aus dem Knysnawalde in Südafrika." *Zeitschr. f. Bot.* **23**, pp. 443–480, Text-figs. 1–8. 1930. (2. 124.)

New species of *Anabaena*, *Closterium*, *Euastrum*, *Spirogyra* and *Xanthidium* are described.

648. Goossens, A. P. "The Genus *Anthephora* Schreb." *Trans. Roy. Soc. S. Afr.* **20**, pp. 189–200. 1932. (2. 125.)

The genus is represented in Africa by about fifteen species extending from Tropical Africa into South-west Africa and through the northern arid districts of the Cape Province into Griqualand West, the Orange Free State, Bechuanaland and the Transvaal. A key is given to the seven species occurring in South Africa. Four new species are described.

649. Brown, N. E. "Contributions to a Knowledge of the Transvaal Iridaceae. Part II." *Trans. Roy. Soc. S. Afr.* **20**, pp. 261–280. 1932. (2. 126.)

The new genera *Tanaosolen*, *Radinosiphon*, *Anaclanthe*, *Curtonus*, *Anomalesia*, *Kentrosiphon*, *Chasmanthe* and *Anapalina* are described and new species and specific combinations are published in the genera *Crocosmia*, *Gladiolus*, *Pentamenes*, *Homoglossum* and *Oenostachys*.

650. Dixon, H. N. "*Ptychomitriopsis* Dix., gen.nov. Ptychomitriacearum." *Journ. of Bot.* **69**, pp. 284–285. 1931. (2. 127.)

A new genus discovered at Zoutpansberg, Transvaal, and Windhoek, South-west Africa.

651. Smith, C. A. "*Palmstruckia* of the Flora Capensis." *Bull. Misc. Inf. Kew*, pp. 154–156. 1931. (2. 128.)

The new name *Thlaspeocarpa* is proposed for *Palmstruckia* Sond. non Retz.

652. Wakefield, E. M. "Fungi Exotici. XXVII." *Bull. Misc. Inf. Kew*, pp. 201–206, 4 Text-figs. 1931. (2. 129.)

New species of *Septoria*, *Septogloeum* and *Pucciniopsis* are described from South Africa.

653. Bullock, A. A. "The Genus *Kraussia*." *Bull. Misc. Inf. Kew*, pp. 254–257. 1931. (2. 130.)

A new species is described from the Transvaal.

654. *The Flowering Plants of South Africa*, II. Pls. 401–430. 1931. (2. 131.)

This contains descriptions of new species in the genera *Crassula* and *Lachenalia* by E. P. Phillips, in the genera *Hessea*, *Polyxena* and *Massonia* by W. Barker, in the genus *Stapelia* by I. Verdoorn and in the genus *Homeria* by L. Bolus.

655. Bolus, L. "Plants New or Noteworthy." *S. Afr. Gard. and Country Life*, pp. 13–14, 51, 55, 77, 247, 281–282, 293 and 367–369, 5 Figs. and 1 Photo. 1931. (2. 132.)

Descriptions of new species in the genera *Ornithogalum, Cotyledon, Cyrtanthus, Ixia, Hesperantha, Babiana, Gladiolus* and *Homeria* with some ecological notes.

656. Barnes, G. "Plants New or Noteworthy." *S. Afr. Gard. and Country Life*, pp. 77, 228 and 234, 1 Fig. and 1 Photo. 1931. (2. 133.)

Descriptions of new species of *Cyrtanthus* and *Veltheimia*.

657. Lewis, G. J. "Ixia." *Journ. Bot. Soc. S. Afr.* **17**, pp. 13–16, Pl. IV. 1931. (2. 134.)

Notes on the geographical distribution of *Ixia*.

(3) AUSTRALIA AND TASMANIA (COLLABORATOR, V. S. SUMMERHAYES)

658. van Steenis, C. G. G. J. "A Revision of the Queensland Bignoniaceae." *Proc. Roy. Soc. Queensland, Brisbane*, **41**, pp. 39–58, 2 Text-figs. February 12th, 1930. (3. 46.)

The family Bignoniaceae is represented in Queensland by six genera and twelve species. Keys to the genera and species are provided together with complete descriptions, citation of all specimens seen, and miscellaneous notes.

659. Ewart, A. J. *Flora of Victoria.* Pp. 1257. 1 Coloured Plate, 349 Text-figs. H. J. Green, Government Printer, Melbourne. 1930. (3. 47.)

This flora deals with the Pteridophytes and Phanerogams. A general introduction touches on the climate, naturalised aliens, and other minor points. Keys to the families, genera and species are provided. Under each genus and species is a short description and also notes on geographical distribution, times of flowering, and sometimes ecological notes. For trees and other plants of economic importance information about the timber, honey, etc. is supplied.

660. Cunningham, G. H. "The Gasteromycetes of Australasia. X. The Phallales, Part 1." *Proc. Linn. Soc. New South Wales, Sydney*, **56**, pp. 1–15, Plates 1–2, 1 Diagram. May 15th, 1931. (3. 48.)

This part deals with the Phallaceae, including three genera in Australia, namely, *Mutinus, Ithyphallus* and *Dictyophora*. A key to the genera is given, while under each genus and species are descriptions, notes on distribution, etc.

661. Cunningham, G. H. "The Gasteromycetes of Australasia. XI. The Phallales, Part 2." *Proc. Linn. Soc. New South Wales, Sydney*, **56**, pp. 182–200, Plates 8–10. July 15th, 1931. (3. 49.)

In this second part the families Clathraceae (six genera) and Claustulaceae (one genus) are described. The treatment is as in Part 1.

662. Cunningham, G. H. "The Gasteromycetes of Australasia. XII. The Genus *Scleroderma.*" *Proc. Linn. Soc. New South Wales, Sydney,* **56**, pp. 277–287, Plates 15–16, 6 Text-figs. October 15th, 1931. (3. 50.)

Five species in all are recognised. A key for identification and descriptions are provided, while notes on geographical distribution and ecology are added.

663. Cunningham, G. H. "The Gasteromycetes of Australasia. XIII. The Genus *Pisolithus.*" *Proc. Linn. Soc. New South Wales, Sydney,* **56**, pp. 288–291, Plate 17. October 15th, 1931. (3. 51.)

Two species are dealt with in this paper, descriptions and notes on geographical distribution being given.

664. Fraser, L. "The Reaction of *Viminaria denudata* to increased Water Content of the Soil." *Proc. Linn. Soc. New South Wales, Sydney,* **56**, pp. 392–406, Plate 22, 18 Text-figs. December 15th, 1931. (3. 52.)

Viminaria denudata is a leguminous switch plant, possessing long terete phyllodes but no true leaves except in the early stages. It grows normally in well-aerated soils, but can survive a condition of soil saturation for extended periods. It reacts to these conditions in definite ways: (*a*) by the production of both upright and knee-bend pneumatophores or breathing roots, in whose parenchymatous tissue an extensive aerating system is present; (*b*) by the production of a secondary aerenchyma in submerged roots from a phellogen arising in the pericycle. Bacterial nodules may also have a covering of secondary aerenchyma except at their growing points.

(4) NEW ZEALAND (COLLABORATOR, V. S. SUMMERHAYES)

665. Laing, R. M. "The New Zealand Species of *Gigartina*, Part 2. (Foliose Forms.)" *Trans. New Zealand Institute, Wellington,* **62**, pp. 134–155, Plates 16–19, 15 Text-figs. September 30th, 1931. (4. 38.)

This portion of the paper, dealing with the foliose forms in the genus, includes only five species, which are, however, very polymorphic. Detailed descriptions and discussions of each species are provided. At the end is an artificial key to all the species of *Gigartina* described including also the non-foliose forms dealt with in Part 1.

666. Cunningham, G. H. "Sclerodermaceae of New Zealand." *Trans. New Zealand Institute, Wellington,* **62**, pp. 115–119, Plates 13–15. September 30th, 1931. (4. 39.)

Three species belonging to two genera are described and figured.

(7) INDIA, BURMA AND CEYLON (COLLABORATOR, R. J. D. GRAHAM)

667. Singh, J. A. "Description of West Khandesh Forest Division." *Indian Forester, Allahabad,* **57**, pp. 71–74. February, 1931. (7. 128.)

A brief description of an area south of the Tapti river in Bombay Presidency.

668. Singh, J. "Hoshiapur Forest Division." *Indian Forester, Allahabad,* **57**, pp. 121–124. March, 1931. (7. 129.)

A brief description of an area south of the Beas river in the Punjab.

669. Davis, D. "Sal Regeneration Fellings." *Indian Forester, Allahabad,* **57**, pp. 153–157. April, 1931. (7. 130.)

Reference is made to the papers by Osmaston (353), and Smythes (448) and a plea made for the maintenance of a light middle story of miscellaneous species.

670. Chaturvedi, M. D. "The regeneration of Sal in the United Provinces." *Indian Forester, Allahabad,* **57**, pp. 157–166. April, 1931. (7. 131.)

An analysis of factors favouring sal regeneration in the U. P. and in Nepal gives the following indications: (1) periodic light fires improve the edaphic factor and destroy the leaf barrier which forms between seed and soil, (2) freedom from weeds is due to a light overwood of miscellaneous species, and (3) this furnishes the ideal conditions for natural regeneration.

671. Vaz, E. T. C. "A short description of Kolaba Forest Division." *Indian Forester, Allahabad,* **57**, pp. 180–184. April, 1931. (7. 132.)

A brief description of a district lying between the Arabian Sea and the Western Ghats.

672. Parker, R. N. "The Andaman Marblewood." *Indian Forester, Allahabad,* **57**, pp. 209–211, Plate 10. May, 1931. (7. 133.)

Diospyros marmorata is described as a new species.

673. Gorrie, R. Maclagan. "Notes on *Pinus Gerardiana.*" *Indian Forester, Allahabad,* **57**, pp. 211–215, Plates 11 and 12. May, 1931. (7. 134.)

Occurring in Afghanistan and Baluchistan and again in a more easterly area in the upper valleys of the Ravi, Chenab and Sutlej, *Pinus Gerardiana* is absent from the area between. Up to 8000 ft. it is confined to the hottest and rockiest aspect. With increasing drought it extends uphill and occupies the better aspects extending to 11,000 ft. The more important plants in each zone are indicated.

674. Glover, H. M. "A short note on ecological changes in the forests of the Eastern Circle, Punjab, and on the need for a scientific survey of the soil flora of regeneration areas." *Indian Forester, Allahabad,* **57**, pp. 325–340. July, 1931. (7. 135.)

A very general paper emphasising the need for investigating the soil flora in forests.

675. Laurie, M. V. "Teak and its Lime Requirements." *Indian Forester, Allahabad*, **57**, pp. 377–381, Plate 18. August, 1931. (7. 136.)

In the Anamalai Hill, Madras, teak of fine quality grows on slightly acid soil markedly deficient in lime. A physical soil factor rather than a chemical one (598) is suggested in Madras and in Burma, this factor in Burma possibly being associated with limestone formations.

676. Parker, R. N. "*Piptanthus* in the Himalaya." *Indian Forester, Allahabad*, **57**, pp. 381–382. August, 1931. (7. 137.)

The remarks on the Indian species of *Piptanthus* in the Botanical Magazine under tab. 9234 are criticised. *Piptanthus leiocarpus* Stapf, is considered a synonym of *P. laburnifolius* Stapf. The Eastern Himalayan species is still unnamed.

677. Fateh Mohammad, M. "The Bamboo forests of Hoshiapur district, Punjab." *Indian Forester, Allahabad*, **57**, pp. 491–512, Plate 26. October, 1931. (7. 138.)

678. Stracey, P. D. "A short note on the uncovering of Sal regeneration in grass in the Goalpara Forest Division, Assam." *Indian Forester, Allahabad*, **57**, pp. 513–515, Plate 27. October, 1931. (7. 139.)

An account of an experiment in freeing Sal seedlings by cutting the surrounding grass.

679. Garland, E. A. "Poona Division." *Indian Forester, Allahabad*, **57**, pp. 520–526. October, 1931. (7. 140.)

An account of the strip of land between the Western Ghats and the Indian Ocean lying to the south of Bombay city. In the heavy rainfall area a type of evergreen forest formation exists and two climatic climax formations are found. *Memecylon edule* is the dominant species at high elevations, and *Terminalia* spp. and *Mangifera indica* at lower levels. In the central area with less rainfall deciduous forests predominate. *Terminalia tomentosa* dominant on better soil and *Anogeissus latifolia* and *Ougenia dalbergioides* on poorer soils of the upper slopes with *Boswellia serrata* on dry southern or western slopes. On lower slopes with deep soil there is pure teak. In the eastern area of low rainfall thorn forests with *Zizyphus Jujuba*, *Acacia latronum* and *Prosopis spicigera* occur.

680. Osmaston, A. E. "The Natural Regeneration of Silver Pine (*Abies* Pindrow)." *Indian Forester, Allahabad*, **57**, pp. 589–599. December, 1931. (7. 141.)

Observations from ten plots in the Kulu division are given. The subsoil was gneiss and an average depth of 2 in. of humus was recorded. A list showing the frequency and constancy of associated plants is given, ten being placed as characteristic of soils favourable to regeneration. Observations on ten plots of deodar showing natural regeneration are also given. The subsoil was mica schist and the average depth of humus $\frac{3}{4}$ in. A list of associated plants is given, ten being placed as characteristic of soils favourable to regeneration.

681. Burns, W. "An experiment in the Improvement of Forest Grass Land." *Indian Forester, Allahabad*, **57**, pp. 601–609, Plate 31. December, 1931. (7. 142.)

The paper includes a list of plants found in the thorn forest near Poona in which *Boswellia serrata* is the dominant tree.

682. Blatter, E. and McCann, C. "A new Indian species of *Begonia*." *Journ. Ind. Bot. Soc. Madras*, **10**, No. 1, pp. 27–28, Plate 1. January, 1931. (7. 143.)

Begonia phrixophylla is described.

683. Ghose, S. L. "Five more Myxophyceae from Burma." *Journ. Ind. Bot. Soc. Madras*, **10**, No. 1, pp. 35–37, Plate 2. January, 1931. (7. 144.)

Five blue-green algae are described from Burma including *Tolypothrix limbata* var. *cylindrica* and *Scytonema leptobasis* which are new.

684. Blatter, E. and McCann, C. "Two new *Utricularias* from the Western Ghats." *Journ. Ind. Bot. Soc. Madras*, **10**, No. 2, pp. 122–125, Plates 1–4. April, 1931. (7. 145.)

U. equiseticaulis and *U. ogmosperma* are described and figured.

685. Blatter, E. and Fernandez, J. "Waziristan Mosses." *Journ. Ind. Bot. Soc. Madras*, **10**, No. 2, pp. 145–153. April, 1931. (7. 146.)

The mosses represent 12 families and 31 genera, the bulk of the species being those of moderate altitudes in the Himalayas with a sprinkling of European and Western Asiatic types. *Leptopterigynandrum brevirette* and *Brachythecium microsericeum* are new.

686. Raizada Mukat Behari. "Contribution to 'Duthie's Flora of the Upper Gangetic Plain' from the neighbourhood of Dehra Dun." *Journ. Ind. Bot. Soc. Madras*, **10**, No. 2, pp. 155–158. April, 1931. (7. 147.)

Twenty-six plants are listed.

687. Dixit, S. C. "Some Charophyta from Salsette." *Journ. Ind. Bot. Soc· Madras*, **10**, No. 3, pp. 205–208, Figs. 1–3. July, 1931. (7. 148.)

Seven species are listed including *Chara succinata* recorded in India for the first time. Notes on this plant are given.

688. Bose, Rakhal Das and Dixit, P. D. "Studies in Indian Barleys. II. Root system." *Ind. Journ. Agric. Sci. Calcutta*, **1**, part 1, pp. 90–108, Fig. 4. February, 1931. (7. 149.)

Root systems of 30 types were studied and fall into four classes depending on the character of the shallow and deep roots. Shallow-rooted types are earlier in maturity, more erect in earlier stages and belong to localities with abundant soil moisture.

689. Blatter, E. and Millard, W. S. "Some beautiful Indian Trees." *Journ. Bombay Nat. Hist. Soc.* **35**, pp. 60–65, Col. Plates 11 and 12, Plates 11 and 12, Text-fig. 5, June, 1931; pp. 289–296, Col. Plates 13 and 14, Plates 13–15, Text-fig. 6, October, 1931. (7. 150.)

Cassia fistula, C. renigera, C. javanica and *Crataeva Nurvala* are illustrated and described.

690. Blatter, E. and McCann, C. "Another new *Ceropegia* from the Western Ghats." *Journ. Bombay Nat. Hist. Soc.* **35**, Plate 1. October, 1931. (7. 151.)

Ceropegia hispida collected near Panchgani is figured and described.

691. Blatter, E. "New species of Indian Plants." *Journ. and Proc. Asiatic Soc. Bengal*, Calcutta, **26** (New Series), No. 1, pp. 339–366. March, 1931. (7. 152.)

The plants described come from the Bombay and Madras Presidencies and Mount Abu. They include *Thalictrum obovatum, Cleome asperrima, Spergula rosea, Indigofera monosperma, Smithia oligantha, Oldenlandia clausa, O. Sedgwickii, Justicia heterocarpoides, Strobilanthus Hallbergii, Dicliptera abuensis, Lepidagathis bandraensis, L. submitis, Cardanthera anomala, Limnophila polystachyoides, Euphorbia panchganiensis, Blyxa echinospermoides, Curcuma inodora, C. purpurea, Kaempfera Evansii, Pancratium Donaldi, Chlorophytum glaucoides, Arisaema longecaudata.*

692. Brühl, P. "A census of Indian Mosses." *Records Botanical Survey India*, Calcutta, **13**, Nos. 1 and 2, pp. 1–134, and pp. 1–152. 1931. (7. 153.)

The list includes species reported from the Indian Empire, Ceylon, the Malay Peninsula, the Malay Archipelago, Siam, Cochin China, Anam, Tonkin, Formosa, Turkestan, the Caucasus, Kurdistan, Persia and Afghanistan, with notes on the collection, preservation and identification of mosses and a Key to the genera recorded with notes on the distribution. A list of the species incorporated in E. Levier's Indian exsiccata as far as they are not mentioned in the second edition of Engler and Prantl's *Pflanzenfamilien* is given.

693. Fischer, C. E. C. "*Flora of the Presidency of Madras.*" Part 9, pp. 1532–1687. London, 1931. (7. 154.)

Commelinaceae, Juncaceae, Palmaceae, Pandanaceae, Typhaceae, Araceae, Lemnaceae, Triuridaceae, Alismaceae, Aponogetonaceae, Potamogetonaceae, Najadaceae, Ericaulaceae and Cyperaceae are included in this part.

694. Barrington, A. H. M. "Forest Soil and Vegetation in the Hlaing Forest Circle, Burma." *Burma Forest Bulletin*, No. 25. (Ecology Series, No. 1), pp. 1–42, Figs. 1–11, Appendices 1–6, pp. 39–95. Rangoon, 1931. (7. 155.)

Situated in a section of the Irrawaddy drainage area the circle stretches from Allanmyo in the North to Insein in the South—a distance of 240 miles with an average width of 35 miles.

Details of the climate appear in Appendix 1. Mean annual temperature 81° F. with rain between May and October ranging from 32 inches in the North to over 100 inches in the South. Details of soil analysis are given in Appendices 2, 3 and 4. Water retention and texture index-number are selected (Fig. 1) as giving the best mechanical value of a soil. Fifty-three plots were chosen for the survey, samples being taken to five or six feet. The botanical census of each plot is given in Appendices 5 and 6.

The seasonal downpour produces a climax of forest growth and five types of Monsoon forest are represented in the samples plots.

(1) Dry Dipterocarp forest with at least one species of *Dipterocarpus* among dominant trees. The society is open, contains few bamboos and the soil is either sandy or heavy calcareous where *Diospyros burmanica* and *Terminalia tomentosa* compete with *Dipterocarpus*. Characteristic plants are *Gardenia obtusifolia, Vernonia teres, Heterophragnum sulfureum, Clerodendron serratum, Ischaemum ciliare*, and *Pollinia articulata*. Consociations are *Dipterocarpus tuberculatus*, Teak and *Pentacme suavis*.

Dipterocarpus tuberculatus is dominant on coarse sand, soils with low texture index and a very little colloidal water, with rainfall 35–47 inches. Important species are *Buchanania latifolia, Cephalostigma paniculata, Aporosa macrophylla, Andropogon fastigiatus, Aristida Adscensionis* and *Cycas siamensis*.

Teak is dominant on soils closely allied to the above with a rainfall rather less than 40 inches. All the soils are definitely acid. The absence of definitely characteristic species suggests this is an unstable type. *Pentacme suavis* in the North ranks second to *Dipterocarpus tuberculatus* on fine sands which are stiffer at the surface than below. Characteristic species are *Harrisonia Bennettii, Alysicarpus bupleuriflorus, Bauhinia diphylla, Crotalaria capitata, Desmodium gyrans, Uraria cordifolia, Strobilanthus roseus* and *Andropogon caricosus.*

(2) Dry mixed deciduous forest is the climax association except in the South. The soils are varied but all have low water retention. Teak on sand and Teak with *Acacia Catechu* on medium heavy and calcareous soils are important with *Dendrocalamus strictus* the typical undergrowth.

(3) Lower mixed forest without bamboos and *Terminalia tomentosa* as dominant is represented on three plots on alluvium. The soils are acid and sour. *Schleichera trijuga, Lagerstroemia tomentosa* are characteristic. It is possible that the plots are unstable and may revert to dry or moist mixed forest.

(4) Moist mixed deciduous forest with Teak and *Xylia dolabriformis* as important trees is the climax in the 80–95 inch rainbelt. *Daedalacanthus montanus* and *Neuracanthus tetragonostachys* are characteristic and *Bambusa polymorpha* the typical bamboo. The soils are deep loams with optimum colloidal water at the sticky point. Transitional types with *Shorea robusta* and *Dipterocarpus turbinatus* verging toward dry Dipterocarp occur on soils resembling lateritite. These soils are deficient in Calcium with a vertical development and enrichment zone at 1–2 feet. *Terminalia tomentosa* is dominant on soils in some way less satisfactory than those that produce Teak and *Xylia* without it.

(5) Lateritite associations show two sub-divisions, the Rangoon lateritite and the *Xylia* lateritite associations.

The first is a complex form of lower mixed on the verge of becoming evergreen Dipterocarp. Dominant trees are *Holarrhena antidysenterica, Litsaea sebifera, Dolichandrone stipulata, Eugenia* spp. and *Grewia Microcos* with consociations of *Careya arborea* and *Homalium tomentosa. Allophyllus* sp., *Milletia atropurpurea* and *Ixora cuneifolia* are characteristic trees, and *Calamus viminalis* the most constant undergrowth.

The soils stiffen rapidly from coarse sand to loam or sandy clay loam where drainage is checked.

Xylia lateritite association, a special example of lower mixed deciduous forest, is dominated by *Xylia dolabriformis* with *Mallotus philippinensis* and *Panicum nodosum* as characteristic species. The soils are better drained than the above as they are less coarse at the surface and do not stiffen so much. The general distribution of Teak, *Xylia* and *Terminalia* is given in Fig. 11. Teak occurs naturally in all associations except lateritite. *Xylia* is more confined and demands soils with a favourable proportion of moisture to texture and avoids calcareous soils. *Terminalia* is confined to ill-balanced soils and is probably favoured by a high percentage of lime. It is probably excluded from better soils by one or other of the above.

695. Bhola, Mathura Prasad and **Hussain, Md. Shaukat.** "Taungya in the Gorakhpur Forest Division." Bull. 4, United Provinces Forest Dept. (7. 156.)

The bulletin gives an account of the method of artificial regeneration Taungya adopted. The regeneration of sal has been made easy and the quality of growth has been improved.

696. Coventry, B. O. *Wild flowers of Kashmir.* Series III, pp. 100 and Introduction, Appendix and Index 29. Col. Plate 50. London, 1930. (7. 157.)

The appendix gives the months of flowering of the species illustrated.

(8) TROPICAL AND NORTH AFRICA (COLLABORATOR, E. MILNE-REDHEAD)

697. Christy, Cuthbert. "Liberia in 1930." *The Geographical Journal*, **77**, No. 6, pp. 515–540, Map 1. June, 1931. (8. 72.)

The author, who has had many years' experience in Tropical Africa, was Chairman of the International Commission of Inquiry in Liberia (1930). The Commission did not penetrate into the interior and the information about the country itself and the vegetation is not necessarily first hand. No new facts are given as to the physical geography. The country is regarded as being under closed forest from a few miles from the coast to a depth of 150 miles. Thence grass woodland occurs with the slopes of the Mandingo Plateau, which rises to about 2500 ft. The greater part of the paper is devoted to history and politics.

698. Hitchcock, A. S. "A Botanical Trip to South and East Africa." *The Scientific Monthly*, **31**, pp. 481–507. December, 1930. (8. 73.)

A semi-popular account of a journey through Southern Rhodesia, Eastern Tanganyika, Kenya and Uganda, made with one of the parties of the British Association for the Advancement of Science after the meetings in South Africa in July and August, 1929. The general vegetation is very briefly referred to and the paper is copiously illustrated by good photographs, especially of the mountain vegetation on Kilimanjaro.

699. Bigorgne, J. "La Forêt de Madagascar." *Revue de Botanique Appliquée*, Paris: *Actes et Comptes Rendus de l'Association Colonies-Sciences*, No. **66**, pp. 249–255. December, 1930. (8. 74.)

The productive economic value of the forests are considered to be very poor, and destruction, chiefly by fire, has been very extensive. The forest types are based on P. de la Bathie's *La Végétation Malgache*. The chief types are (1) the evergreen forests of the east, (2) the deciduous forest of the west, (3) the xerophilous forest of the south, (4) the mangroves. Brief descriptions are given of each of these types. The remainder of this, the first instalment of the article, is devoted to a discussion of the species of economic value.

700. *Tanganyika Territory, Department of Tsetse Research Co-ordination Report*, No. **4**, April 1st, 1930 to September 30th, 1931, pp. 1–12. The Government Printer, Dar-es-Salaam. Price 1s. (8. 75.)

A summary is given of the recent investigations into the autecology and synecology of *Glossina morsitans*. Short progress reports are given of the work at the Kikori Entomological Station, Shinganga Field Experiment Station, Itundwe Barrier Planting Station and Itundwe Vegetation-Poisoning Station. Brief notes are also given on biological control and co-operation work with the Veterinary Department. No definite conclusions are drawn as to the result of the year's work, which is a record of experiments in operation which have been discussed in previous annual reports.

701. Hancock, G. L. R. and **Soundy, W. W.** "Notes on the Fauna and Flora of Northern Bugishu and Masaba (Elgon)." *Journ. East Afr. and Uganda Nat. Hist. Soc.* No. **36**, pp. 165–183, Plates 1–6. 1931. (8. 76.)

A brief description of the position and altitude of the areas concerned, including a discussion of the more widely used African name "Massawa" for Mount Elgon is followed by an account of the insects found in rock pools and streams. Observations of the morning and evening ground temperature are included. Sections dealing with the insects and plants of

the Bamboo and higher forests, and of the Alpine zone, follow, the dominant plants of different habitats being mentioned by name. The plates are from photographs (two on each plate), and illustrate the various habitats and·the type of country; Plate IV shows an excellent picture of a specimen of *Lobelia elgonensis* almost as tall as the native carrier standing beside it, and Plate V shows much branched *Senecio elgonensis* near the lake below Jackson's Summit (13,650 ft.). The paper concludes with a full bibliography and two appendices consisting of lists of species collected by the two authors and others who are mentioned in the text.

702. Anon. "On Kilimanjaro. Flora of an African Mountain." *The Times*, p. 13. January 2nd, 1931. (8. 77.)

A semi-popular account of the flora and vegetation of Mt Kilimanjaro in Tanganyika Territory. The main belts of vegetation are the forest belt extending to about 8000 ft. altitude, the mountain meadows of tussock grasses and flowers reaching to about 10,500 ft. and the alpine region of rocky ground clothed with scrub, *Helichrysum* spp. and other woolly xerophytes which extends to the limit of phanerogamic vegetation, namely to between 13,000 and 14,000 ft.

703. Hubbard, J. W. The Isoko Country, Southern Nigeria. *The Geographical Journal*, 77,. No. 2, pp. 110–122, 6 Photographs, 1 Map. February, 1931. (8. 78.)

A general description of the densely forested country which lies about 60 miles east of Warri. The annual inundations during the rainy season render this tract of country impassable except by canoe.

704. Whitehouse, Lieut.-Commander **G. T.** The Langia-Acholi Mountain Region of the Sudan-Uganda Borderland. *The Geographical Journal*, 77, No. 2, pp. 140–159, 6 Photographs, 1 Map. February, 1931. (8. 79.)

The author is a surveyor in the service of the Sudan Government and in 1927 carried out the necessary surveys to make a map of this little-known mountainous country. A general account of the topography is given, and the origin and customs of the native tribes are discussed. The Government measures for stamping out sleeping sickness by removing the population to a height above the forest country is described. The author then details the account of a tour he made through these mountains, and his ascent of Mt Kineti, the highest peak of the Anglo-Egyptian Sudan. References to literature dealing with the vegetation are given.

705. Hutchinson, J. "*Hypericum lanceolatum.*" *Kew Bull.* 1931, p. 224. April, 1931. (8. 80.)

This *Hypericum* is recorded from the Cameroons Mountain for the first time. It is found at altitudes between 4000 and 10,000 ft., and reaches its maximum development, as a tree about 40 ft. high, at 7000 ft. On the upper grassy slopes it is only a shrub.

706. Hutchinson, J. "General Smuts' Botanical Expedition to Northern Rhodesia, 1930." *Kew Bull.* 1931, pp. 225–254, 3 Maps and 5 Figures. May, 1931. (8. 81.)

In this picturesque account of a botanical collecting expedition from Pretoria to Abercorn, by road, brief mention is made of the vegetational types that were met with, namely the "Mopane" bush, *Acacia-Combretum* bush, high veld, and *Brachystegia* forest. Many of the more striking plants, which were encountered, are mentioned.

707. Cotton, A. D. "The Arborescent Senecios of the Virunga Mountains." *Kew Bull.* 1931, pp. 289–297, with Map. June, 1931. (8. 82.)

This paper includes a brief summary of all the botanical expeditions to the Virunga Mountains, with special reference to the *Senecio* vegetation. A valuable list of references to the literature of the Virunga Mountains is appended.

708. Collenette, C. L. "North-eastern British Somaliland." *Kew Bull.* 1931, pp. 401–414, 1 Map and 2 Photographic Plates. August, 1931. (8. 83.)

The topography and the climate of the area are described, and some valuable figures are given. The principal biotic factors are natives, domestic animals, locusts, and fire. The vegetations of the three topographical areas are described. (1) The coastal plain with only a few stunted *Acacia* spp. and with *Tamarix nilotica* and *Suaeda fruticosa* on the seashore. (2) The inland plateau, which is divided into two types, that of the limestone rocky soil, with *Balanites orbicularis*, and 4 *Acacia* spp. dominant, and that of the sandy soil with *Acacia spirocarpa* the only common tree, and *Zizyphus Hamur* and *Tamarix nilotica* also dominant. (3) The Al Hills where the vegetation varies from the relatively rich *Croton confertus*, *Bridelia somalensis*, *Maerua sessiliflora*, *Balanites aegyptica*, *Acacia spirocarpa*, *Zizyphus Hamur*, etc. association in the valleys of the southern foot hills, to the dominance of *Buxus Hildebrandtii* of the highest zone. A comparison is made with the vegetation of the Surud Mountain, which lies about 120 miles farther to the west, where *Juniperus procera* is dominant at the higher elevations to the exclusion of the *Buxus*. The herbaceous vegetation of this mountain is said to be poorer than that of the Al Hills. The edaphic vegetations of seepage cliffs and shaded ravines are briefly described.

(9) TROPICAL AMERICA AND WEST INDIES (COLLABORATOR, R. C. McLEAN)

709. *Report of the Conservator of Forests, Trinidad and Tobago*, 1929. *Council Paper* No. 57 of 1930. Trinidad. 1930. (9. 16.)

Mainly administrative, but contains an outline of the nature of the local rain forest and of the investigations on climatic and soil conditions which are on hand.

710. Martyn, E. B. "A Botanical Survey of the Rupununi Development Company's Ranch at Waranama, Berbice River." *Agric. Journ. British Guiana*, Georgetown, **4**, Pt 1, pp. 18–25, 2 Plates. March, 1931. (9. 17.)

The ranch is about 60 miles inland and 80–90 ft. above sea level, with an area of about 70 sq. miles. The survey was made in September, the chief object being to explore the possibilities of the open savannah as a pasturage for cattle. The chief constituents were four grasses and two sedges, in proportions varying slightly from place to place, influenced by soil variations. Two main soil types occur, (*a*) sandhill, (*b*) brown sand. On (*a*) *Trachypogon plumosus* is dominant (about one-quarter of all individuals). Associated are *Axonopus aureus*, *Andropogon leucostachyus*, *Aristida setifolia* and *Rynchospora pterocarpa*. On (*b*) the vegetation is thinner, but the *Rynchospora* and also *Stenophyllus coniferus* are relatively more abundant. All are highly xeromorphic and are liable to periodic fires. Bushes are represented by *Byrsonima coccolobaefolia* and *Curatella americana*. The best pasturage is afforded by slightly depressed areas, called pans, where additional grasses occur. Forest or bush areas rise like "oases" out of the savannah, the transitional zone being rarely more than 2–3 yards wide. Small-leaved Myrtaceae and Malpighiaceae are predominant, while in swampy areas the Aeta Palm (*Mauritia flexuosa*) forms pure belts of palm forest. Areas of pure quartz sand occur, bearing patches of xerophilous scrub, 15–20 ft. high, known as "Muri" and dominated by *Clusia nemorosa*.

711. Follett Smith, R. R. "An Analysis of Pasture Grasses of the Colony."
Agric. Journ. Brit. Guiana, **4**, p. 43, March, 1931. (9. 18.)

Analyses of Guantemela Grass (*Tripsacum* sp.) and of Wynne Grass (*Melinis minutiflora*).

*712. Hardy, F., Akhurst, C. G. and **Griffith, G.** "Studies in West Indian
Soils, III. The Cacao Soils of Tobago." Supplement to *Tropical Agriculture*,
8, No. 2, pp. 23, 1 map. February, 1931. (9. 19.)

The method of soil examination mainly consisted in the examination and sampling of
profiles exposed in artificial pits 6 ft. deep. The total number of profiles studied was 35, cover-
ing three-quarters of the area of the island. Examinations were completed at the Imperial
College of Tropical Agriculture, Trinidad. The soils originate from three parent rock types:
(1) Igneous Rocks, (2) Metamorphic Sedimentary Rocks, (3) Unaltered Sedimentaries of
Tertiary or post-Tertiary Age. The soil profiles of residual and transported soils of each type
are described. They are mostly immature, due to removal of the original top soil by erosion
after clearance of the ground. Only one was truly lateritic and this was the only one taken
in a true forest area at high elevation.

* Numbers I and II of this series appeared before the commencement of these Abstracts.
They are given here for convenience of reference.

I. "The Soils of Dominica; their Genesis and Fertility considered in Relation to Reaction."
Hardy, F., *West Ind. Bull.* **19**, pp. 86–123. 1922.

II. "The Soils of Montserrat; their Natural History and chief Physical Properties."
Hardy, F., *West Ind. Bull.* **19**, pp. 189–213, 1922.